Protecting the larger fish: an ecological, economical and evolutionary analysis using a demographic model

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Protecting the larger fish: an ecological, economical and evolutionary analysis using a demographic model

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Abstract

Many marine fish stocks are reported as overfished on a global scale. This overfishing not only removes fish biomass, but also causes dramatic changes in the age and size structure of fish stocks. In particular, targeting of the larger individuals truncates the age and size structure of stocks. Recently, there is increasing evidence that this size-selective fishing reduces the chances of maintaining populations at levels sufficient to produce maximum sustainable yields, the chances of recovery/rebuilding populations that have been depleted/collapsed and may causes rapid evolutionary changes in life-history traits of exploited fish stocks. The main purpose of the present PhD thesis is to gain an understanding of the role of the larger fish in a population , from three different areas of science specifically, ecology, economics and evolution. An extended classical single species age and size-structured model is used and the whole analysis is focussed on two theoretical stocks with life history traits typical of a large and long-lived species (W_∞=20 kg) and of a small and short-lived species (W_∞=0.5 kg).

Several fish stock-specific studies, both field observations and experimental studies, indicate that not only do the larger and older females spawn more eggs in each spawning event than smaller-younger females, but their eggs are larger and of higher quality in terms of survival than the eggs from smaller-younger females, a phenomenon known as maternal effects. However, most traditional management models assume that all female fish contribute equally per unit biomass to future recruitment. The second chapter of the thesis considers the influence of maternal effects on recruitment and on the commonly used reference points: the fishing mortality rate corresponding to the maximum sustainable yield (F_{MSY}) and the fishing mortality where the population collapses (F_{crash}). Our results demonstrate that the incorporation of maternal effects into the recruitment equation will not result in better scientific advice for a stock being managed to achieve maximum

sustainable yield (MSY). It may however be important to account properly for maternal effects for collapsing populations.

The third chapter develops an ecological-economic evaluation tool to explore the impact of the choice of a recovery scenario on the time needed to recover the stock and on the net benefit generated by the fishery during the recovery period and beyond. This is achieved by merging a classical age-structured model for a single-species population with an economic cost-evaluation framework. One of the recovery scenarios pay particular attention to the larger individuals. Our results suggest that the larger fish does not matter much neither from an economic nor from an ecological perspective. Only if there is a high fishing pressure during the recovery period can a preservation of the larger individuals reduce recovery time significantly.

The fourth and last chapter is focused on fisheries induced evolution and the consequent changes in yield. We attempt to evaluate the capability of the larger fish to mitigate the evolutionary change on life-history traits caused by fishing, while also maintaining a sustainable annual yield. This is achieved by calculating the expected selection response on three life-history traits: size at maturation, growth rate, and reproductive investment under two different fishing scenarios, with and without a maximum-size limit. We find that each life-history trait responds differently to the introduction of size-selective fishing regulations, and that only a reduction in fishing mortality will reduce the magnitude of the selection response on all traits. The consequent changes in fisheries yields are less than 10 % per decade. We conclude that size-based management regulations alone are unable to mitigate fisheries induced evolution on all evolving traits.

The main conclusion of this thesis is that in most cases protecting the larger fish does not matter much for the population. High fishing pressure is the primary concern about the sustainability of the fisheries, population recovery and the evolutionary changes in life-history traits.

Abstract

Mange marine fiskebestande er rapporterede som overfiskede på globalt plan. Dette overfiskeri fjerner ikke kun fiskebiomasse, men giver også anledning til dramatiske ændringer i alder, størrelse og struktur af fiskebestandene. Specielt når man målrettet fisker de større individer påvirker det alder, størrelse og struktur af bestandene. I den seneste tid har man set tegn på at det selektive fiskeri, hvor man målretter sig mod at fiske de større fisk, mindsker chancerne for opretholdelse af bestanden på et niveau, der er tilstrækkeligt til at give maksimalt bæredygtigt udbytte. Chancen for at genopbygge bestanden når den er kollapset mindskes tillige, og fiskeriet kan forårsage hurtige evolutionære ændringer i vigtige livshistorietræk. Det vigtigste formål med denne ph.d.-afhandling er at opnå en forståelse af de større fisks rolle i en bestand ud fra tre forskellige områder af videnskabelig tænkning; økologi, økonomi og evolution. Der er anvendt en udvidet, klassisk enkeltarts-model baseret på art, alder og størrelse, og hele analysen er fokuseret på to teoretiske med livshistorietræk typisk for en stor art med lang levetid og en lille og kortlivet art.

Flere fiskebestand-specifikke undersøgelser - både feltobservationer og eksperimentelle undersøgelser - tyder på, at større og ældre hunner gyder flere æg i hver gydning end mindre og yngre hunner, men deres æg er også større og af højere kvalitet med hensyn til overlevelse end æg fra mindre yngre hunner, et fænomen kendt som maternelle effekter. Men de fleste traditionelle forvaltningsmodeller antager, at alle hunner bidrager ligeligt pr biomasse til fremtidige rekrutter. Det andet kapitel af afhandlingen diskuterer indflydelsen af maternelle effekter på rekruttering og på de almindeligt anvendte referencepunkter: den fiskeridødelighed, der svarer til det maksimale bæredygtige udbytte (Fmsy) samt fiskeridødeligheden hvor bestanden kollapser (Fcrash). Vores resultater demonstrerer, at indarbejdelsen af maternelle effekter ind i rekrutteringsligningen ikke vil resultere i

bedre videnskabelig rådgivning om en bestand, der forvaltes for at nå et maksimalt bæredygtigt udbytte (MSY). Det kan dog være vigtigt at kunne redegøre ordentligt for maternelle effekter for kollapsede bestande.

Det tredje kapitel udvikler et økologisk-økonomisk vurderingsværktøj til at undersøge effekten af et scenarier, af den tid det kræver tid til at gendanne en bestand og af den netto fordel genereret ved fiskeriet i løbet af restitutionsperioden og videre frem. Dette opnås ved at sammenlægge en klassisk alders-struktureret model for en enkelt-arts bestand med en økonomisk cost-evaluerings-"ramme". Et af genopretningsscenarierne er særlig opmærksom på de større individer. Vores resultater tyder på, at større fisk ikke har så meget betydning hverken fra et økonomisk eller fra et økologisk perspektiv. Kun hvis der er et højt fiskeritryk i løbet af gendannelses perioden kan en bevarelse af de større individer reducere genopretningstiden betydeligt.

Det fjerde og sidste kapitel er fokuseret på fiskeri induceret evolution og de deraf følgende ændringer i udbytte. Vi forsøger at vurdere evnen til at de større fisk kan hindre de evolutionære forandringer på livet-historie træk forårsaget af fiskeri, mens man samtidig fastholder et bæredygtigt årligt udbytte. Dette opnås ved at beregne det forventede selektionsrespons på tre livshistorie egenskaber: størrelse ved gydemodning, vækstrate, og reproduktiv investering under to forskellige fiske scenarier, med og uden en grænse for maksimal størrelse. Vi finder, at hvert livhistorietræk reagerer forskelligt på indførelsen af reglerne omkring størrelsesselektivt fiskeri, og at kun en reduktion i fiskeridødeligheden vil reducere størrelsen af selektionsrespons på alle træk. De deraf følgende ændringer i fiskeriets udbyttet er mindre end 10% per årti. Vi konkluderer, at størrelsesbaseret regulering alene ikke er tilstrækkeligt til at mindske fiskeriets påvirkning af evolution på alle træk.

Hovedkonklusionen i denne tese er, at i de fleste tilfælde har det mindre betydning for populationen at beskytte større fisk. Højt fiskeritryk er den primære bekymring for bæredygtigheden af fiskeriet, bestandens genoprettelse og evolutionære ændringer i livshistorietræk.

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Chapter 1

Introduction

1.1 The State of World Fisheries

The state of world's fisheries and the views of fisheries scientists has changed over the last two centuries. In 1803, Thomas Huxley, then president of the Royal Society of London, delivered the opening address of the Great International Fisheries Exhibition under the title "Are fisheries exhaustible?" The Huxley's answer was a certain no. "Probably all the great sea fisheries are inexhaustible; that is to say that nothing we do seriously affects the number of the fish," declared. The world's fisheries were dominated by Huxley's views during more than a century.

In the middle of the twentieth century, the term "inexhaustible" was still used to describe the state of the world fisheries. In 1955, Francis Minot, then director of the Marine and Fisheries Engineering Research Institute, in Woods Hole, Massachusetts, in Hawthorne & Minot, 1955 he observed "we do not know the ocean well enough. Much must still be learned. Nevertheless, we are already beginning to understand that what it has to offer extends beyond the limits of our imagination" . In 1964, a report from the US Department of the Interior predicted that fishery yield could be "increased at least tenfold without endangering fish stocks". Three years later, the department revised its estimate and declared that the yield could be increased not by a factor of ten but by a factor of forty, to two billion tons a year. As Michael L. Weber observed (Weber, 2001), the nineteen-nineties U.S. policy was predicted "on the belief that the ocean's productivity was almost limitless."

The support of the belief that our planets natural resources were endless abounded until 1968 when the ecologist Garrett Hardin published an influential article titled "The Tragedy of the Commons" (Hardin, 1968). He declared that continuing to believe on "the inexhaustible

resources of the oceans," bring species after species of fish and whales closer to extinction. In 1997, the total world catch peaked at an estimated 93 million tons and in subsequent years, the total catch was steadily declining. It is estimated that the total catch is dropping by around five hundred thousand tons a year. It is believed that this reduction is an indication that humans are now fishing more than what the ocean can produce and the explanation of why fisheries would collapse starts being in the public domain.

Nowadays, most of the worlds most important fish stocks have now been fished to the limit of sustainability. Stocks have collapsed in nearly one-third of sea fisheries, and the rate of decline is accelerating. There will be virtually nothing left to fish from the seas by the middle of the century if current trends continue, according to a major scientific study. It is not difficult to see what we have done. Within the last decade or so, we have seen the 40,000 unemployed fishers after the collapse of the northern cod (Harder, 2003). We have seen jellyfish blooms around the world (Purcell *et al.* , 2001). We have seen innumerable scientific articles that predict an austere future for marine fisheries (Pauly *et al.* , 2003). It is time of enormous concern about the future of the world fisheries. Perhaps the most alarming report came in late 2006, when Boris Worm, a marine conservation ecologist at Dalhousie University in Nova Scotia, reported in Science that for 29 percent of currently fished species, the catch had dropped to less than 10 percent of the historical maximum. If the trends continue, he reported, all fisheries around the globe will collapse by 2048 (Worm *et al.* , 2006).

As an old Chinese proverb says, "Give a man a fish and he will eat for a day. Teach a man to fish and he will eat for the rest of his life" . But we have seen that teaching a man to fish sustainably is another concern today.

1.2 The alleged importance of the larger fish

For many years, fisheries scientist believed that the best way for the conservation of fish stocks was to protect the small fish and put selective fishing pressure on large fish. The reasoning was to allow smaller, younger individuals to grow up to reproductive age to help to provide a sustainable fish resource now and into the future. In recent years, however, the importance of the larger individuals in a fish stock has received increasing attention, in particular due to the realization that these individuals produce both a higher quantity and quality of eggs in terms of survival than smaller and younger females. On the other hand, it has long been known that small fish have much higher natural mortality rates than larger fish, because as fish

grow larger, they have fewer fish bigger than themselves to prey on them. Some scientists are now beginning to propose the idea that the larger individuals are essential for the successful maintenance of many fish populations (Berkeley *et al.* , 2004a; Field *et al.* , 2008; Longhurst, 2002; Marteinsdottir & Steinarsson, 1998; Scott *et al.* , 1999, 2006).

This size-selective fishing pressure on the larger fish causes dramatic changes in the age and size structure of fish stocks (Berkeley *et al.* , 2004b; Jackson *et al.* , 2001; Longhurst, 2002) and may result in a number of negative impacts on fish spawning. These negative impacts include: a shortening and change in timing of the spawning season (Berkeley *et al.* , 2004a; Scott *et al.* , 2006; Wieland *et al.* , 2000), a decrease in the production of eggs and larvae (Berkeley *et al.* , 2004b; Birkeland & Dayton, 2005), a decrease in the average survival potential of larvae (Berkeley *et al.* , 2004a; Conover & Munch, 2002), and a reduction in genetic heterogeneity (Law, 2000). These factors could reduce the chances of maintaining populations at levels sufficient to produce maximum sustainable yields, the chances of recovery/rebuilding populations that have been depleted/collapsed (Birkeland & Dayton, 2005; Field *et al.* , 2008) and may causes rapid evolutionary changes in life-history traits of exploited fish stocks (Conover & Munch, 2002; Darimont *et al.* , 2009; Law, 2007; Ricker, 1981; Walsh *et al.* , 2006).

In summary, we can say that taking greater care of the larger individuals within fish populations seems especially benefitial. However, in most stocks as a result of the current size-selective fishing pressure, the larger fish have become scarce. It is therefore unclear whether the relatively small number of these larger individuals can contribute substantially to improve fisheries management.

1.3 A review of fish stock models

"Fish are born, they grow, they reproduce and they die whether from natural causes or from fishing. That's it. Modelers just use complicated (or not so complicated) math to iron out the details".

Andrew B. Cooper.
A Guide to Fisheries Stock Assessment: From Data to Recommendations.

Fish stock models range from the simple holistic models that intend to capture all biological processes in a simple equation such as surplus production models, to the detailed and elaborate

age-structured demographic models that include several sets of equations and which intend to give a more realistic representation of fish population dynamics.

1.3.1 Surplus production models

These models consider the stock globally, in particular the total abundance (in weight or in number) and study its evolution, the relation with the fishing effort, etc. These models are among the simplest and most widely used in stock assessment. They are easy to use because they require only two or three types of data. These models are very flexible and have different variations; the Schaefer, Fox, and Pella-Tomlinson models are some of the best known.

1.3.1.1 The Schaefer model

The Schaefer model is the most commonly used among Surplus production models. This model is based precisely on the logistic population growth model. Verhulst published in 1838 (Verhulst, 1838) the logistic equation that describes population growth based on the following mathematical expression,

$$dB/dt = rB(t) \cdot \left(1 - \frac{B(t)}{K}\right), \tag{1.1}$$

where r is the intrinsic rate of population growth, $B(t)$ is population biomass in time t and K is the carrying capacity of the environment. The logistic model specifies how the growth rate of a population varies with population size described as a sigmoid curve.

The first application of this law in fisheries was by (Graham, 1935) who employed this growth law in an analysis of the effect of World War I on the abundance and landings of demersal fishes from the North Sea, but the model became very popular following the publication of Schaefer, 1954:

$$B_{t+1} = B_t + rB_t(1 - \frac{B_t}{K}) - C_t \tag{1.2}$$

where $C_t = FB_t$ and F is the instantaneous fishing mortality.

The management parameters of importance from the Schaefer model are: $MSY = rK/4$, $B_{MSY} = K/2$ and $F_{MSY} = r/2q$.

1.3.1.2 The Fox model

The Fox model (Fox, 1970), is based on the Gompertz growth model and the model equation is:

$$B_{t+1} = B_t + rB_t(1 - \frac{lnB_t}{lnK}) - C_t \tag{1.3}$$

The model is supposed to be more "realistic" because it assumes that the population can never be totally driven to extinction, something that sounds intuitive but is probably wrong in light of the severe depletion of fishery resources in recent years and the well-documented human-caused terrestrial species extinctions. The management parameters of the Fox model are: $MSY = rKe^{-1}/lnK$, $B_{\mathrm{MSY}} = Ke^{-1}$, $F_{\mathrm{MSY}} = r/qlnK$.

1.3.1.3 Pella and Tomlinson model

Pella & Tomlinson, 1969 proposed a generalized model that can take any shape, including that of the Schaefer (m=2) and Fox (m=1) models.

$$\frac{dB}{dt} = rB - \frac{rB^m}{K} \tag{1.4}$$

However, there is a price to be paid for this "improvement" and that is having to estimate an additional parameter (m) to fit the model to the data. This model is not much more useful because despite its "flexibility" the fit will probably be worse than with either the Schaefer, 1954 or Fox, 1974 models as there is a known inverse relationship between the number of parameters to be estimated and the performance of the models (see Hilborn & Walters, 1992).

The advantage of surplus production models is that data requirements are modest compared with age-structured models, yet surplus production models can yield critical information for assessment and management such as estimates of virgin and current biomass, level of depletion of the population, MSY, optimal effort (F_{MSY}). A disadvantage of surplus production models is the lack of biological reality, they assume that all the processes occurring in a population can be captured by the simple processes described above while ignoring the size or age structure of the population and the dynamics of different parts of the population.

1.3.2 Age/size structured demographic models

Demography is the science of populations. Demographers seek to understand population dynamics by investigating two main demographic processes: birth and death. While demography cannot offer political advice on how to tackle demographic change, demographers seek to describe the phenomena related to this change, and to understand their causes. Using reliable data and the statistical processing of these data, modern demographic research embraces many scientific disciplines, including mathematics, economics and other social sciences, geography or biology.

1.3.2.1 The yield per recruit model

This model, first developed by Beverton & Holt, 1957, provides a steady-state (static) view of the population that allows determination of the catch or yield relative to recruitment (catch divided by recruitment, thus the yield per recruit or Y/R name of the technique) that can be obtained from a stock according to different levels of fishing mortality F and age of entry to the fishery.

The model describes the population in terms of the biological processes of growth, recruitment and mortality, and treats the exploited population as the sum of its individual members. It has more biological detail than surplus production models reviewed above but is not as powerful and detailed as the fully age-structured models treated below. Also, it is inferior to surplus production model in the sense that it is static, assumes that there is no dependence between stock size and recruitment, and cannot provide estimates of absolute biomass or be used for making projections of stock size according to different management strategies. Its main utility is that it indicates if the fishery is catching fish at an age that is too early or too late to obtain the maximum biomass relative to recruitment, and whether the level of fishing mortality is adequate.

The yield per recruit equation of Beverton & Holt, 1957 is:

$$\frac{Y}{R} = FW_{\infty}e^{-M(t_c-t_r)}\sum_{n=0}^{n=3}\frac{\Omega_n}{F+M+nK}e^{-nK(t_c-t_0)}(1-e^{-(M+F+nK)(t_1-t_c)}) \quad (1.5)$$

where M is the natural mortality rate, t_0 is the von Bertalanffy parameter that describes age at zero length, t_t is maximum age of fish in stock, k is the von Bertalanffy growth coefficient and the integration constants are: Ω_0=1,Ω_1=-3,Ω_2=3,Ω_3=-1.

The main advantages of the yield per recruit method is that it is relatively simple to implement and does not require historical data on catch and effort. It is a step forward from demographic methods because it tells us within a relatively simple implementation procedure - if we are exploiting fish at the right age (or size), and also if we are fishing at the right intensity. The disadvantages are that the model unrealistically assumes known and constant over all ages and over time natural mortality and stock size; recruitment is constant and can be ignored.

1.3.2.2 The delay-difference model

The delay-difference model was first proposed by Deriso, 1980 and further generalized by Schnute, 1985. It is a clever simplification that allows the inclusion of biological information of the species to be taken into account in a simple way. The model incorporates the four main types of biological information: body growth, recruitment, survival and a measure of age structure. This model belongs to an intermediate class known as partially age-structured models, which represents a step forward from the rather simple surplus-production models that ignore biological processes like recruitment and individual growth, while avoiding the demanding data requirements of the more sophisticated fully age-structured models. The model allows for time lags in the dynamics of the stock, such as are found in species with slow growth and late age of entry to the fishery. This ability to take into account time delay is what gives the model its name of "delay-difference" model.

Following is the original form of the model and it requires seven parameters to predict biomass dynamics and to fit the model to catch and CPUE data Schnute, 1985:

$$B_{\mathrm{t}} = (1+\rho)S_{t-1}B_{t-1} - \rho S_{t-1}S_{t-2}B_{t-2} - \rho w_{k-1}S_{t-1}R_{t-1} + w_k R_t \tag{1.6}$$

An important advantage of this model is that it has a smaller number of model parameters to be estimated in comparison to fully age-structured models. Thus it can be applied to fisheries with limited amounts of data while still offering a more realistic representation of population dynamics.

1.3.2.3 Our demographic model

The model used in this thesis is a classical age-structured population model with a Beverton and Holt stock-recruitment relationship (Beverton & Holt, 1957). The effective number of

parameters in the model have been reduced using size-based scaling relationships and life-history invariants, such that the main parameter describing a certain stock is the asymptotic (maximum) body size W_∞.

Growth is modeled by the von Bertalanffy growth equation (Bertalanffy, 1938) relating weight w to age x. The spawning stock biomass, the total biomass of all sexually mature fish in the population, is $\sum_{x=1}^{X_\infty} N_t(x)w(x)m(x)$, where $N_t(x)$ is the number of fish of age x at time t. Maturation at age $m(x)$ is described by a sigmoid function with 50 % maturation at $\eta_M W_\infty$. Recruitment is assumed to take place once annually and supplies the first age class with recruits. The natural mortality for an individual is a declining function of size, $\mu(w) \propto w^{-1/3}$, which can be described in terms of the ratio between adult mortality M and the von Bertlanffy growth constant M/K as Andersen *et al.* , 2009b. The mortality for an individual because of fishing is described by a sigmoid function with inflection point at $\eta_F W_\infty$. The effect of reducing the fishing mortality on the larger individuals is examined by lowering the fishing mortality to zero for $w > \eta_{Boff} W_\infty$. Fishery yield is determined by Baranov's catch equation (Baranov, 1918).

1.4 Structure of the thesis

The second chapter of the thesis considers the influence of maternal effects on recruitment and on the commonly used reference points: the fishing mortality rate corresponding to the maximum sustainable yield (F_{MSY}) and the fishing mortality where the population collapses (F_{crash}). The third chapter develops an ecological-economic evaluation tool to explore the impact of the choice of a recovery scenario on the time needed to recover the stock and on the net benefit generated by the fishery during the recovery period and beyond. The fourth and last chapter is focussed on fisheries induced evolution and the consequent changes in yield. We attempt to evaluate the capability of the larger fish to mitigate the evolutionary change on life-history traits caused by fishing, while also maintaining a sustainable annual yield.

In the second chapter, the terminology used for the larger and older invividuals is "Boff" (the *Big old fecund fish*). Here, the egg production is proportional to the body size and to the production of surviving eggs and larvae ("egg quality"), so Boff produce both a higher quality and quantity of eggs than smaller and younger females. However, in the third and fourth chapter the terminology used for the larger and older invividuals is "the larger". Here, the egg production is only proportional to body size, so the larger individuals contribute more to future generations than small individuals only due to its larger size.

Chapter 2

The impact of maternal effects on recruitment and fisheries reference points

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Abstract

The targeting of the larger and older individuals truncates the age distribution of fish stocks. Recent evidence indicates that larger and older females produce both a higher quality and quantity of eggs than younger females, a phenomenon known as maternal effects. However, most traditional management models assume that all female fish contribute equally per unit biomass to future recruitment. Here we investigate whether this assumption is valid by calculating the impact of maternal effects both before and after accounting for density-dependent effects. We find that the impact of maternal effects before density-dependent effects is largest for unfished stocks. The influence of maternal effects on fisheries reference points has only a significant impact for the fishing mortality where the stock collapses (F_{crash}), while the fishing mortality at maximum sustainable yield (F_{MSY}) is largely unaffected. Our results demonstrate that incorporation of maternal effects in fisheries advice is most important for stocks where fishing significantly reduces recruitment and suggest that fisheries management strategies which exclude maternal effects may be increasing the vulnerability of these stocks to further decline or delayed recovery.

Key words: fisheries management, life history, maternal effects, age-structured population model, recruitment

2.1 Introduction

Many marine fish stocks are reported as overfished on a global scale (Hilborn *et al.* , 2003; Pauly, 2008; Worm *et al.* , 2009). Overfishing not only removes fish biomass, but also causes dramatic changes in the age and size structure of fish stocks (Berkeley *et al.* , 2004a; Jackson *et al.* , 2001; Longhurst, 2002). In particular, targeting the larger and older individuals (the *Big old fecund fish (Boff)*) truncates the age and size structure of stocks.

Several fish stock-specific studies, both field observations and experimental studies, indicate that not only do Boff spawn more eggs in each spawning event than smaller-younger females, but their eggs are larger and of higher quality in terms of survival than the eggs from smaller-younger females. Moreover the spawning times and durations of individuals having different ages and sizes can differ within populations which could expose eggs and larvae to more/less favorable ocean conditions for survival and growth (Wright & Trippel, 2009). The effect has been demonstrated for cod (*Gadus morhua*) (Kjesbu *et al.* , 1996; Marteinsdottir

& Steinarsson, 1998; Trippel, 1998), haddock (*Melanogrammus aeglefinus*) (Hislop, 1988), black rockfish (*Sebastes melanops*) (Berkeley *et al.* , 2004b) and Winter flounder (*Pseudopleuronectes americanus*) (Buckley *et al.* , 1991). All these studies suggest that age and size of spawners is very important in determining both the number and the quality of eggs produced by a stock. However these studies do not address whether the individual-level effects of large females translate into significant impacts on population dynamics. To do so, one must consider the numbers of those individuals in exploited stocks. In most stocks, the numbers of Boff are usually very low relative to the numbers of younger, smaller females due to both natural and fishing mortality. It is therefore unclear whether the relatively small number of Boff can contribute substantially to production of new recruits even given the documented beneficial effects of such individuals on production and quality of eggs and larvae.

The field evidence for an impact of the Boff on e.g. recruitment is ambiguous. Given the observations of maternal effects on females one might hypothesize that recruitment per spawning stock biomass (*SSB*) would be lowered when the age structure of a stock is skewed towards younger individuals. For example, (Cardinale & Arrhenius, 2000; Jarre-Teichmann *et al.* , 2000; Marteinsdottir & Steinarsson, 1998) observed that diversity of age structure of spawner biomass explained significant variation in recruitment in Icelandic and Baltic cod populations. More recently Venturelli *et al.* , 2009 found that maximum reproductive rates in 25 wild fish stocks representing 25 species were higher when stocks were characterized by Boff individuals than by smaller, younger individuals. However, Morgan *et al.* , 2007 studying American plaice (*Hippoglossoides platessoides*) and Atlantic cod (*Gadus morhua*) stocks found that the influence of spawners' age and size structure on recruitment was not always observed. In addition, a cross-species analysis of the relationship between age and size structure of spawners and recruitment revealed a relationship for some stocks, but not for the majority of them and opposite relationships were also found (Brunel, 2010). These contradictory findings suggest that the importance of the age structure of spawners on recruitment is not fully understood and the effects might differ between species.

One of the main goals in fisheries science and management is maintenance of the stock reproductive potential (i.e. the ability of the stock to produce new recruits) at long-term sustainable levels (Hilborn & Walters, 1992). Thus, given the importance of reproductive potential to scientific advice for fisheries, it is important to understand the role of maternal effects on population dynamics and how such effects may be affected by differences in species' life

history traits. It has therefore been suggested that maternal effects may have to be incorporated more fully into considerations of reference points used in fisheries management advice (Mangel *et al.* , 2010; Morgan, 2008).

This article considers the influence of maternal effects on recruitment and on the commonly used reference points: the fishing mortality rate corresponding to the maximum sustainable yield (F_{MSY}) and the fishing mortality where the population collapses (F_{crash}). The questions addressed here are: how do changes in the age stock structure, e.g. due to not fishing the Boff in a stock influence recruitment and the reference points? What are the consequences of ignoring maternal effects for recruitment and for the reference points?

To do so we use a size/age-based model of fish stock demography and recruitment. The model is general and uses life-history invariants to calculate stock structure and recruitment solely based on a characterization of a fish stock by the asymptotic size of individuals, which is available for most stocks. The impact of maternal effects are considered first on the demography (stock structure) of the stock, and secondly on recruitment. As the strength of the maternal effect is difficult to determine exactly, and as it may vary between species, it is difficult to make a general statement about the importance of maternal effects on the stock level. Therefore we turn the problem around and estimate the impact as a function of the strength of maternal effects (φ), and thereby determine how large a maternal effect leads to a given stock-level response on recruitment and reference points.

2.2 Methods

The model is a classical age structured population model with a Beverton and Holt stock-recruitment relationship (Beverton & Holt, 1957). Size-at-age is described by a von Bertalanffy growth equation (Bertalanffy, 1938), making it possible to relate age and size. The remaining parameters are either described in terms of life-history invariants (Charnov *et al.* , 2001) or related to asymptotic weight, W_∞. In this way the relevant properties of population structure and changes in recruitment due to maternal effects can be calculated for a fish stock characterized by its asymptotic size only.

Growth is modeled by the von Bertalanffy growth equation (Bertalanffy, 1938) relating weight w to age x:

$$w(x) = W_\infty \left(1 - e^{-Kx}\right)^3, \tag{2.1}$$

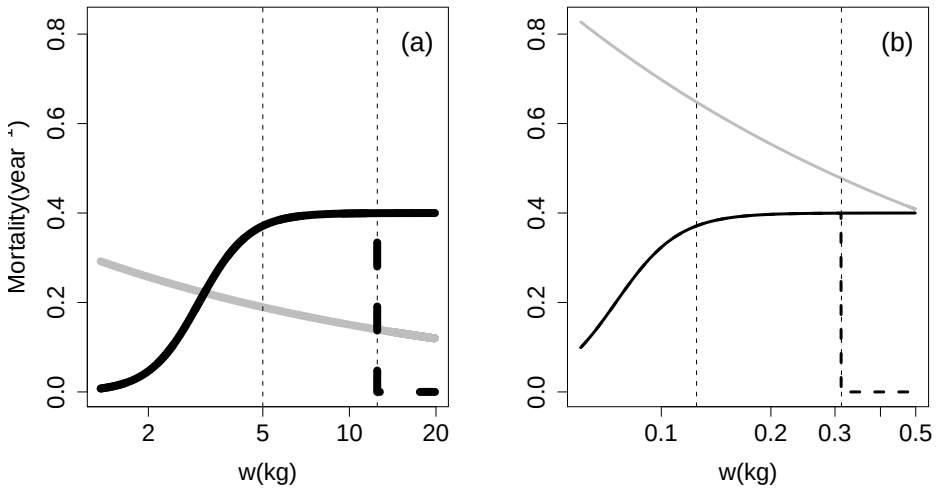

Figure 2.1: Mortality as a function of size for large and long lived species (a) and small and short lived species (b). Grey lines are natural mortality, black lines are fishing mortality of $F = 0.4$ yr^{-1} when fishing is on all sizes larger than $\eta_F W_\infty$, dashed lines are fishing mortality of $F = 0.4$ yr^{-1} when fishing is on intermediate sizes ($\eta_F < w/W_\infty < \eta_{Boff}$). The vertical lines are drawn at maturation size $\eta_M W_\infty$ and at Boff size $\eta_{Boff} W_\infty$.

where K is the von Bertalanffy growth constant. K can be related to asymptotic size as $K = \hbar W_\infty^{-1/3}/3$ where $\hbar$ is a species-independent growth constant (Andersen & Beyer, 2011; Andersen *et al.* , 2009b).

Natural mortality for an individual is a declining function of size, $\mu(w) \propto w^{-1/3}$, which can be described in terms of the ratio between adult mortality M and the von Bertlanffy growth constant M/K as Andersen *et al.* , 2009b (Fig. 2.1):

$$\mu(x) = \frac{1}{3}\hbar\eta_M^{1/3}\left(\frac{M}{K}\right)w(x)^{-1/3}, \tag{2.2}$$

where the life-history invariant η_M is the ratio between size at maturation and asymptotic size (Beverton, 1992).

Fishing mortality is described by a sigmoid function with inflection point at $\eta_F W_\infty$. The effect of reducing the fishing mortality on the Boff is examined by lowering the fishing mortality to zero for $w > \eta_{Boff} W_\infty$ (Fig. 2.1). Fishery yield is determined by Baranov's catch equation

(Baranov, 1918):

$$Y = \sum_{x=1}^{X_\infty} B(x)F(x)\frac{1-e^{-(\mu(x)+F(x))\Delta t}}{(\mu(x)+F(x))\Delta t}, \tag{2.3}$$

where B is the population biomass and $\Delta t = 1$ year.

The number of individuals of age x at time t, $N_{\mathrm{t}}(x)$, is:

$$N(t,x) = N(t-1,x-1)e^{-(\mu(x)+F(x))\Delta t}. \tag{2.4}$$

We have adapted the Beverton and Holt stock-recruitment equation (Beverton & Holt, 1957) to take maternal effects into account. Recruitment is assumed to take place once annually and supplies the first age class with recruits. Maturation at age $m(x)$ is described by a sigmoid function with 50 % maturation at $\eta_{\mathrm{M}}W_\infty$. The Spawning Stock Biomass *SSB*, the total biomass of all female sexually mature fish in the population, is $\sum_{x=1}^{X_\infty} N_{\mathrm{t}}(x)m(x)w(x)$.

Normally maternal effects are disregarded, and the fish egg production is assumed to be proportional to the weight: $P(w) = \alpha w$, where α is the yearly egg production per body mass. Here, maternal effects on recruitment are included by assuming that the contribution of fish of size w is proportional to w^φ: $P_e(w) = \alpha_e w^\varphi$, where φ is a free parameter that characterizes the strength of the various types of maternal effects summarized in the Introduction. Varying φ changes the egg production from being the same at all weights ($\varphi = 1$) to being more and more dependent on weight ($\varphi > 1$). The inclusion on maternal effects through φ is, however, not straightforward to compare a situation where the influence of maternal effects is ignored $\varphi = 1$ with one where maternal effects are taken into account $\varphi > 1$. A decision has to be made upon which size the two yearly egg production rates are equal. We have chosen to assume the size between size at maturation and asymptotic size and this is $\eta_{\mathrm{Boff}}W_\infty$: $P(\eta_{\mathrm{Boff}}W_\infty) = P_e(\eta_{\mathrm{Boff}}W_\infty)$ then, $\alpha_e = \alpha(\eta_{\mathrm{Boff}}W_\infty)^{1-\varphi}$ (Fig. 2.2).

The aim here is to calculate the change in production of surviving eggs from the whole population for different strengths of maternal effects φ. We define the "effective *SSB*" (SSB_{eff}) as a measure which is proportional to the production of surviving eggs and larvae ("egg quality") before density-dependent processes such as competition for a limiting food resource and predation (Myers & Cadigan, 1993).

$$SSB_{\mathrm{eff\,t}} = \sum_{x=1}^{X_\infty} N_{\mathrm{t}}(x)m(x)w(x)^\varphi(\eta_{\mathrm{Boff}}W_\infty)^{1-\varphi}, \tag{2.5}$$

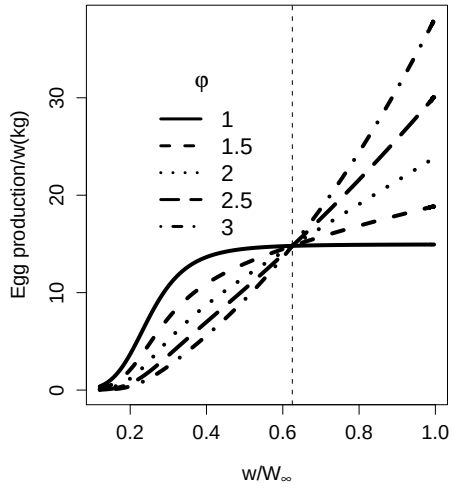

Figure 2.2: Illustration of the effect of changing the strength of maternal effects φ on production of eggs as a function of size. The vertical lines is drawn at Boff size $\eta_{\text{Boff}} W_\infty$.

Recruitment is then given by:

$$R(SSB_{\text{efft}}) = \frac{\alpha SSB_{\text{efft}}}{(1+\alpha SSB_{\text{efft}})R_{\max}}, \tag{2.6}$$

where α is the slope of the recruitment curve at low *SSB* (i.e. egg production at negligible density dependent effects). It has been found from empirical and theoretical analysis to be a declining function of asymptotic size (see Table 2.1), which is in line with cross-species analysis of recruitment (Andersen & Beyer, 2011). $R_{\max}$ is the maximum rate of recruitment at high stock biomass.

The model is iterated until the population reaches a stable age distribution. Parameters are determined from cross-species analyses or from theoretical arguments (Table 2.1). The analysis here assumes homogeneous and stable environmental conditions for all years and seasons within the year, and for all areas where the spawners actually produce their eggs and where the eggs, larvae and juvenile grow and survive to become recruits. The model is run for varying levels of maternal effects φ and with fishing mortality which is either fishing all fish above a lower limit $\eta_F W_\infty$, or only fish of intermediate size $\eta_F < w/W_\infty < \eta_{\text{Boff}}$. In this manner both the impact of maternal effect themselves and the impact of protecting the Boff are explored. The model is run for two theoretical stocks with life history traits typical of a large and long-lived

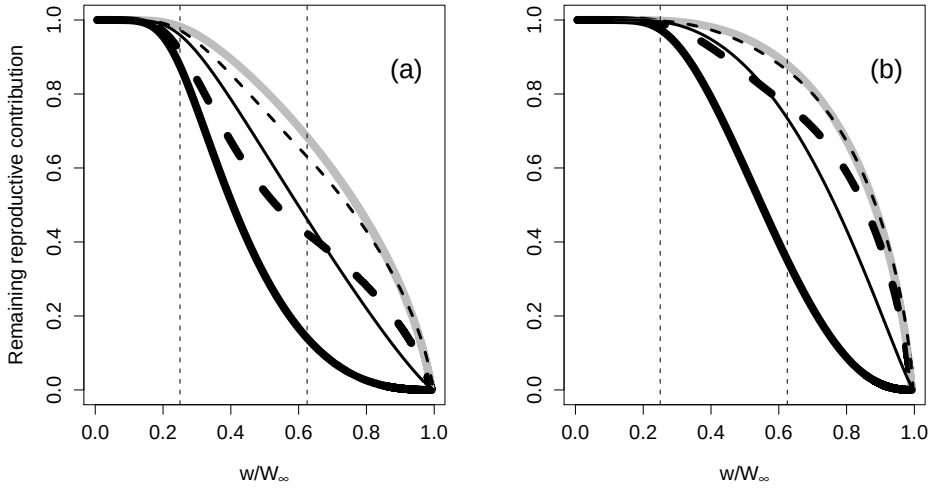

Figure 2.3: The total egg production of all individuals larger than a size w, shown as a fraction of the total egg production of the whole population without maternal effects $\varphi = 1$ (a) and with maternal effects $\varphi = 3$ (b). Large and long lived species (thick lines) and small and short lived species (thin lines). Unfished situation (grey), $F = 0.4$ yr^{-1} on all sizes larger than $\eta_F W_\infty$ (solid) and $F = 0.4$ yr^{-1} on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$ (dashed). The vertical lines are drawn at maturation size $\eta_M W_\infty$ and at Boff size $\eta_{Boff} W_\infty$.

species ($W_\infty = 20$ kg) and of a small and short-lived species ($W_\infty = 0.5$ kg). From now on, we will refer to large and long-lived species as "large" and to small and short-lived species as "small".

2.3 Results

The influence of maternal effects can be divided into the impact due to changes in the age and size structure of the stock and impacts due to the recruitment function.

The exposure to a fishing mortality of $F = 0.4$ yr^{-1} has a quite different impact on the small than on the large species. Because fishing mortality of $F = 0.4$ yr^{-1} relative to natural mortality is much higher for the large species (Fig. 2.1), the stock structure of large species will be more influenced by fishing than smaller species.

The contribution of the Boff to the total reproductive output of the population can be examined by calculating the fraction of total egg production stemming from females larger than a

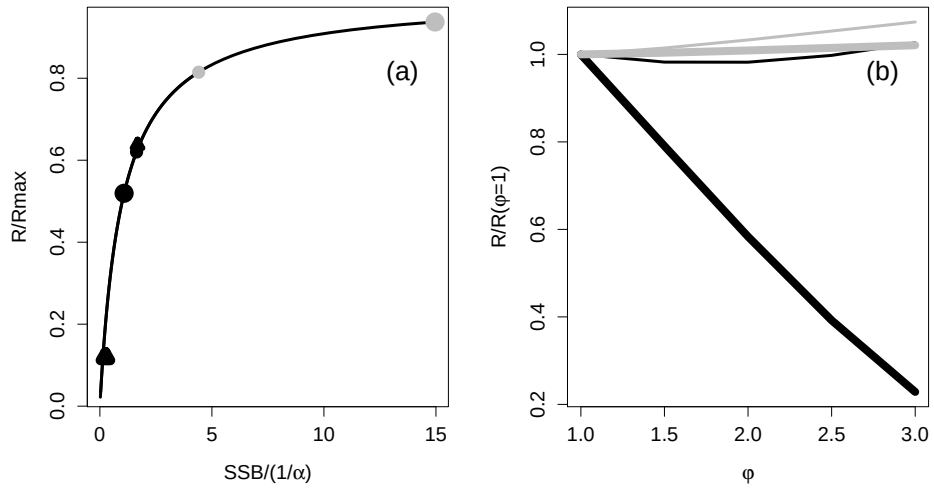

Figure 2.4: Spawning stock-recruit curve (a) and recruitment as a function of the strength of maternal effects (φ) (b). (a) The spawning stock-recruit curve is scaled by the maximum recruitment ($R_{\max}$) and by the value of the $1/\alpha$ to show the stable point for the large and long-lived species (big circles) and small and short-lived species (small circles), for the unfished situation (grey) and fished population ($F = 0.4$ yr^{-1}) without maternal effects ($\varphi = 1$, circles) and with maternal effects ($\varphi = 3$, triangles). (b) For large and long-lived species (thick lines) and small and short-lived species (thin lines). Increase in recruitment for an unfished *SSB* (grey) and when *SSB* is fished at $F = 0.4$ yr^{-1} (black).

given size (Fig. 2.3). This "remaining reproductive contribution" is calculated by dividing the total egg production of all females larger than a given size w ($\sum_{x=w}^{W_\infty} N_t(x)m(x)w^\varphi$) by the total egg production of the entire population ($\sum_{x=w_1}^{W_\infty} N_t(x)m(x)w^\varphi$ where w_1 is the first size group). The influence of the Boff for the egg production is largest in the unfished situation (grey lines) where about 70 % of the egg production originates from the Boff (Fig. 2.3a). When maternal effects are considered (e.g. $\varphi = 3$), the Boff contribute about 90 % of the production of surviving eggs (Fig. 2.3b). For fished populations ($F = 0.4$ yr^{-1}, black) and $\varphi = 1$, less than 14 % of the egg production comes from Boff in the large species population, while for small species about 46 % of the production is from Boff. If $\varphi = 3$, the impact is higher in the small species' population (about 70 %) than for large species' populations (about 35 %). If the Boff are not fished (dashed lines), the impact is higher in the small species' populations, about 63 % of the egg production originates from Boff, while for large species only about 42 % of the production

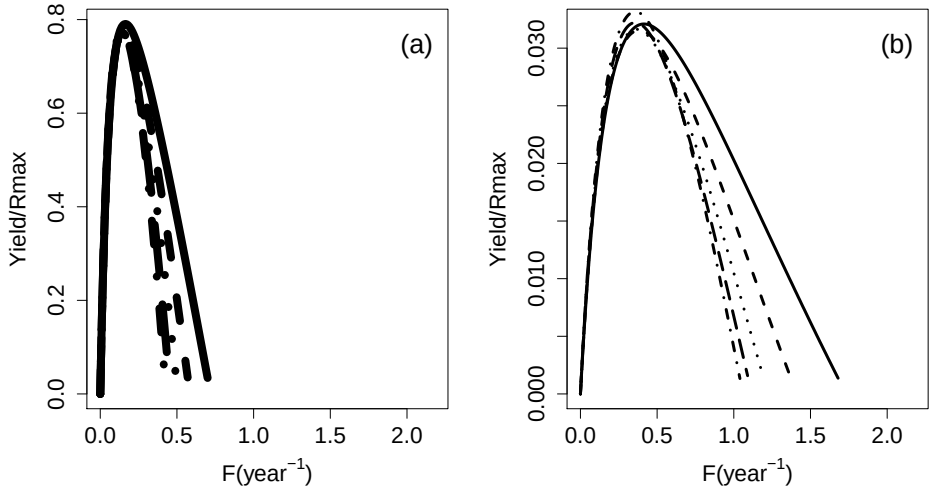

Figure 2.5: Yield as a function of fishing mortality for large and long-lived species (a) and small and for short-lived species (b). Fishing on all sizes larger than $\eta_F W_\infty$; without maternal effects $\varphi = 1$ (solid), with maternal effects $\varphi = 1.5$ (dashed), $\varphi = 2$ (dotted), $\varphi = 2.5$ (longdash), $\varphi = 3$ (dotdash).

is from Boff when $\varphi = 1$. When $\varphi = 3$ the difference between species is smaller, 86 % for the small and 76 % for the large species.

To calculate the effects of production of surviving eggs on recruitment, egg production has to be filtered through the recruitment function. If the recruitment is saturated by high levels of fish recruitment, i.e. $SSB \gg 1/\alpha$, increases in production of surviving eggs due to maternal effects will not have a noticeable impact on recruitment. Even though the recruitment of larger species has a smaller slope at the origin, they have a much larger *SSB* relative to $1/\alpha$ than smaller species, and therefore the end result is that they end higher up on the recruitment curve when the stock is unexploited (Fig. 2.4a). In contrast, exploiting both stocks at $F = 0.4$ yr^{-1} results in a lower *SSB* for the large species than for the small species. As the larger species is harder hit by a given fishing mortality than the smaller species, the recruitment moves further down on the recruitment curve than for the small species especially when maternal effects are taken into account (e.g. $\varphi = 3$).

Maternal effects are taken into account by varying the strength of the parameter φ above the default value of 1 (Fig. 2.4b). Maternal effects are expected to have a significant impact on

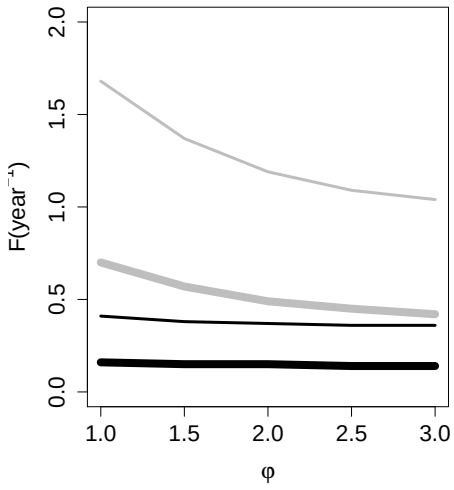

Figure 2.6: Fisheries reference points as a function of the strength of maternal effects (φ). Large and long-lived species (thick lines) and small and for short-lived species (thinner lines). F_{MSY} (black) and F_{crash} (grey).

recruitment only when the stocks are heavily exploited (i.e, when recruitment is substantially limited by *SSB*). With the fishing mortality used in the example the largest species is close to a collapse, and the impact of ignoring the maternal effects is therefore high, because the recruitment capacity of the smallest individuals, which dominate the stock structure (Fig. 2.3a) is overestimated (Fig. 2.2).

The impact of ignoring maternal effects on the fisheries reference points can be examined from a plot of yield vs fishing mortality (Fig. 2.5). The maximum sustainable yield (*MSY*) and the F_{MSY} are insensitive to the whether maternal effects are taken into account or not. However, the incorporation of maternal effects is expected to decrease the F_{crash} i.e. the limit that corresponds to very high value of F, showing a great probability of collapse of the fishery. The relative change in the reference points between small and large species is small (Fig. 2.6).

The importance of the potential increase of the surviving egg production of the largest individuals may be bolstered by a ban on fishing large individuals (Fig. 2.7). Removing fishing mortality on Boff individuals significantly decreases the *MSY* and increases the F_{MSY}. When the Boff in this species are protected, the yield biomass is distributed among smaller age/size classes (from $\eta_{\mathrm{F}} W_\infty$ to $\eta_{\mathrm{Boff}} W_\infty$) so a decrease of the *MSY* is as expected. This result also sug-

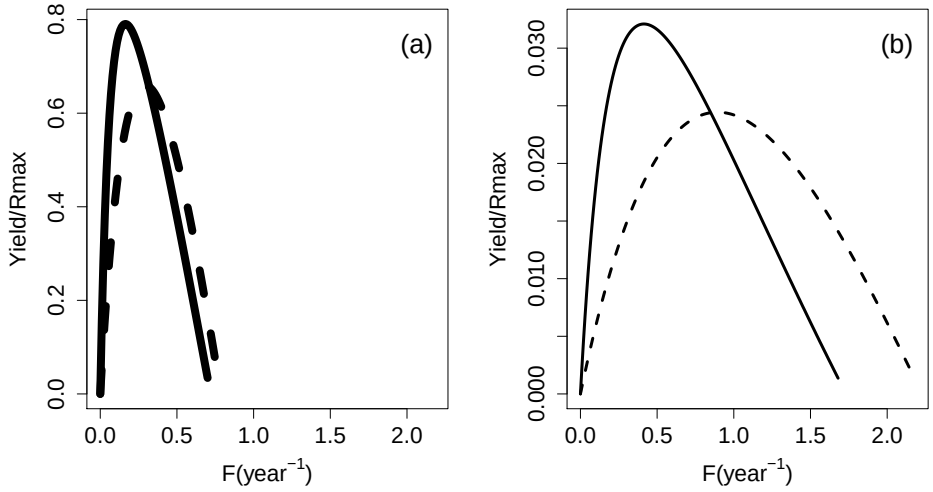

Figure 2.7: Yield as a function of fishing mortality for large and long-lived species (a) and small short-lived species (b). Fishing on all sizes larger than $\eta_F W_\infty$ (solid) and fishing on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$ (dashed). Without maternal effects ($\varphi = 1$).

gests that stocks that have an extended age structure can support a higher rate of exploitation, if the Boff are not exploited.

2.4 Discussion

We have incorporated maternal effects in a classical age-structured fish stock model and in the Beverton and Holt recruitment function to analyze the effect of age and size structure on recruitment and reference points. We have used the Beverton and Holt recruitment function because it ensured stable population structure. Had we used a non-monotonic recruitment curve, e.g. the Ricker curve, we may have had unstable (oscillating or chaotic) population dynamics for high values of *SSB*, for low fishing mortalities and large species. However, qualitatively the results are expected to be similar with the two recruitment functions. We have generalized previous calculations made on specific stocks such that our calculation covers all species characterized by their asymptotic size, and shown the results for two typical life histories (a small and short-lived species and large and long-lived species).

To assess the impact of maternal effects, both the impact due to the age and size structure

and the recruitment-spawner biomass relationship should be accounted for. The former is easily assessed, but the recruitment curve may be difficult to estimate. We showed that the stock-recruitment function is expected to have a large dampening effect for large species, so it should not be ignored when the effect of maternal effects are assessed. Ignoring the recruitment curve (e.g. O'Farrell & Botsford, 2006) will lead to an overestimation of the importance of maternal effects.

Even though recruitment dampens the effect of maternal effects on the unfished stocks, the influence of maternal effects on recruitment is expected to be bigger for fished stocks. This is because fished stocks are expected to have lower relative recruitment (lower on the recruitment curve) than unfished stocks, and therefore changes in the effective *SSB* have a higher impact on the total population. The results are consistent with Brunel, 2010, whose meta-analysis provides a positive correlation between three indices of age structure and the variability in recruitment, but not with recruitment in absolute terms. Venturelli *et al.* , 2009 moreover, using both a population model and a meta-analysis show that maternal quality can have a strong effects on a population's maximum reproductive rate. However, in this study they did not include changes in the age and size stock structure.

As pointed out by Murawski *et al.* , 2001 for Georges Bank cod, ignoring maternal effects is not expected to have a high impact on long term fishing mortality rate that would allow for stock replacement. Similarly, another study for Pacific Ocean Perch (*Sebastesalutus*) Spencer *et al.* , 2007 found F_{MSY} to be insensitive to the presence of maternal effects. And for the specific example of black rockfish O'Farrell & Botsford, 2006 found that an addition of the maternal age effect had small fisheries implications. These findings are also in accordance with our general prediction that F_{MSY} is largely unaffected by maternal effects. However, the fishing mortality where a stock collapses (F_{crash}) is strongly affected. Our analysis here demonstrated that this is because the influence of maternal effects are particularly important when the stock is close to a crash, where the recruitment function is decreasing most rapidly as a function of *SSB* (see Fig. 2.4b). In nature, this situation of declining spawner biomass is often accompanied by age and size structures which are dominated by small, young adults whose effective egg production is lower than if the remaining spawner biomass was composed of Boff.

In conclusion our study suggests that the incorporation of maternal effects into the recruitment equation has little importance when interpreting and forecasting population dynamics and will not result in better scientific advice for a stock being managed to achieve maximum

sustainable yield (MSY). It may however be important to account properly for maternal effects for collapsing populations.

Acknowledgements

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Table 2.1: Model parameters

Symbol	Parameter	Value
Control parameters:		
F	Fishing mortality	free (0,...,2 yr^{-1})
W_∞	Asymptotic (maximum) size	free (0.5 kg, 20 kg)
X_∞	Maximum age	free (10 years, 30 years)
φ	Strength of maternal effects	free (1.1,...,3)
Fundamental parameters:		
$\hbar$	growth constant[a]	16.2 $g^{1/3}$ yr^{-1}
M/K	Mortality/growth relation[b]	0.95
η_M	Ratio between size at maturation and W_∞[c]	0.25
η_F	Ratio between size at 50 % F and W_∞	0.15
η_{Boff}	Ratio between size where Boff start and W_∞	0.625
α_0	Constant in recruitment equation[d]	$6{\cdot}10^4 yr^{-1}$
R_{max}	Maximum rate of recruitment at high stock biomass	-
Derived parameters:		
K	von Bertalanffy growth constant	$\hbar W_\infty^{-1/3}/3$
α	Productivity parameter of the stock recruitment equation [d]	$\alpha_0(\frac{W_\infty}{0.01})^{-2.3/3}$

[a] At 10° Andersen *et al.* , 2008

[b] Andersen *et al.* , 2009b

[c] Beverton, 1992

[d] Hall *et al.* , 2006

Chapter 3

Ecological and economic consequences of different recovery scenarios of depleted stocks

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Abstract

There is an increasing trend in the percentage of fish stocks throughout the world that are over-exploited, depleted or recovering and for which effective recovery plans are required. This paper develops an ecological-economic evaluation tool to explore the impact of the choice of a recovery scenario on the time needed to recover the stock and on the net benefit generated by the fishery during the recovery period and beyond. This is achieved by merging a classical age-structured model for a single-species population with an economic cost-evaluation framework. Recovery scenarios for two stocks with a large and a small asymptotic body size are evaluated and compared. The economic results indicate that the difference between choosing one recovery scenario over the other is limited. It has been shown that the larger individuals in a stock have a higher reproductive success than smaller and younger fish, and therefore a recovery plan may have to pay particular attention to these large individuals. The larger fish does not matter much neither from an economic nor from an ecological perspective. Only if there is a high fishing pressure during the recovery period can saving of the larger individuals reduce recovery time significantly.

Key words: age-structured population model, Cost Benefit Analysis (CBA), Net Present Value (NPV), fisheries management

3.1 Introduction

The United Nations Food and Agriculture Organization (FAO), which monitors the state of the world fisheries, has estimated that in 2008 more than one-quarter of marine fish stocks were either overexploited, depleted or recovering from depletion (28 %, 3 % and 1 % respectively). This is the lowest percentage recorded since the mid-1970s. While reviews of a range of world-wide recovery plans (Caddy & Agnew, 2004; Wiedenmann & Mangel, 2006) show examples of stocks recovering from overfishing (Hart, 2003; Pipitone *et al.* , 2000; Richards & Rago, 1999; Terceiro, 2002), there are many other examples of slow or unsuccessful stock recovery, even with substantial reductions in fishing mortality (Hutchings & Myers, 1994; Polachek, 1990; Shelton & Healey, 1999; Tegner *et al.* , 1996). Given the declining condition of fish stocks, there is no doubt that the current state of world fisheries gives cause for concern, therefore, effective recovery plans are required (Murawski, 2010; Worm *et al.* , 2009).

Seen from a production perspective, the goal of fisheries management is to exploit the fished stock in a manner that maximizes the yield. In terms of fisheries reference points, this means that the fishing mortality should be the one that generates the maximum sustainable yield F_{MSY}. If a stock is in a depleted state ($F > F_{\mathrm{MSY}}$), then the question for management is to draw a plan which will achieve F_{MSY}. However, the success of a fishery management plan depends (at least) on two different requirements: achieving the economic objectives of the fishery and achieving the fisheries reference point. The successful recovery of a species depends on a multitude of different conditions: fishing effort, climatic conditions, changes in the ecosystem, by-catch from other fisheries, and changes in recruitment dynamics. The effect that can most readily be quantified is the direct effects of fishing on stock structure and recruitment. The goal in this paper is to examine how different fishing patterns and pressures affect the recovery of a depleted fish stock to levels that can produce the maximum sustainable yield (MSY) in the ecologically and economically most attractive fashion.

The time it takes to recover a depleted stock depends on two factors: the time to reach maturation and the speed at which the spawning stock biomass (SSB) can be recovered to a level where recruitment is limited mainly by density-dependent effects. For a large and long-lived species (large asymptotic body size) the age at maturation is higher than for a small and short-lived species. Considering this effect only, the large species is expected to recover slower than a small species. On the other hand, a large species has a larger reproductive potential than a small species, even when the longer time to reach maturation is taken into account (Andersen & Beyer, 2011; Andersen *et al.* , 2008). Considering reproduction only, it is therefore expected that a large species will recover its reproductive potential faster than the small species. These two effects (time to reach maturation and reproductive capacity) therefore vary in opposite directions for species with large and small asymptotic body size. An evaluation of the time it takes for a population to recover therefore requires a quantitative analysis that weights the time to reach maturation against the reproductive potential of the mature individuals. The evaluation of a recovery plan should take other factors than pure ecological factors into account. In particular the economical consequences may be assessed by a cost-benefit analysis. As a individual typically have a higher value per weight than a smaller individual (Zimmermann *et al.* , 2011), the economical consequences will also depend on the size structure of the stock in a systematic fashion. Hence, the question addressed here is: what are the ecological and economic consequences of different recovery plans for small and large species?

3. Ecological and economic consequences of different recovery scenarios of depleted stocks

A stock that is exploited at high rates for a sufficient duration of time may enter a collapsed state in which its recruitment is limited by the biomass of spawners and their production of eggs. There have been several examples of collapsed states where the stocks have not rebuilt even in a complete closure of the fishery due to Allee effects (Hutchings & Reynolds, 2004). However, the case we are addressing here is a stock whose spawner biomass has been lowered such that it produces a lower yield from the fishery than it potentially could, but whose recruitment is not necessarily substantially limited by spawner biomass. We are therefore mainly addressing a "recovery" of a "depleted" stock ($SSB < 10\ \%\ SSB_{\text{unfished}}$) to produce maximal yield, in contrast to the "rebuilding" of a "collapsed" stock ($SSB < 1\ \%\ SSB_{\text{unfished}}$) where recruitment is limited by spawner biomass or egg production.

It is well known that the larger individuals in a stock (the *Big old fecund fish (Boff)*) spawn more eggs in each spawning event than smaller individuals due to their larger size. Therefore, one would expect a lower recruitment per spawning stock biomass when the age structure of the spawners is skewed towards younger individuals. Age-structure and the larger fish appears, thus, to play a key role on both the recruitment success and sustainability of exploited fish populations. Moreover, the selective removal of the larger fish probably contributes to the difficulty that some populations experience in recovery from overfishing (Birkeland & Dayton, 2005; Field *et al.* , 2008). However, even though the larger fish may produce more eggs, there are also much fewer of the larger fish in the stock. There is therefore a need to make quantitative analyses which weighs the higher quantity of the eggs of the larger fish against the larger quantity of the smaller fish to determine the importance of the larger fish for the whole stock. The issue that we would like to emphasize in this paper is the contribution of the larger fish in a recovery plan.

To explore the impact of the choice of a recovery plan we use a size/age-based life history model for describing the demography of the fish stock, and an economical cost-benefit analysis (CBA) to describe the long-term economic consequences of recovery. The ecological impact of the recovery plan is described by the time needed to recover the stock to levels that can produce the MSY, and the economic impact is described by the net benefits generated by the fishery (NPV) during the recovery period and beyond. We analyse three different recovery plans: (1) Fishery closure (i.e. instantaneous fishing mortality rate is zero); (2) Lowering fishing mortality ($F \leq F_{\text{MSY}}$) but fishing only on intermediate sizes (i.e. saving the larger individuals); (3) Lowering fishing mortality ($F \leq F_{\text{MSY}}$), but fishing all size groups. The model is general and uses life-history invariants to calculate stock structure and recruitment solely based on a

characterization of a fish stock by the asymptotic size of individuals, which is available for most stocks. The analysis of this paper is on two theoretical stocks with life history traits typical of a large and long-lived species (W_∞=20 kg) and of a small and short-lived species (W_∞=0.5 kg).

3.2 Model formulation

The ecological model used to evaluate the time to recover under different scenarios is a classical age-structured population model with a Beverton-Holt stock-recruitment relationship (Beverton & Holt, 1957). The effective number of parameters in the model have been reduced using size-based scaling relationships and life-history invariants, such that the main parameter describing a certain stock is the asymptotic (maximum) body size W_∞. The principles of the model is described in the second chapter of this thesis and Andersen & Beyer, 2011, so in this chapter the main principles here are provided briefly, and the model equations are given in Table 3.1 and parameters are given in Table 3.2.

Growth is modeled by the von Bertalanffy growth equation (Bertalanffy, 1938) relating weight w to age x (Fig. 3.1a). The spawning stock biomass, the total biomass of all sexually mature fish in the population, is $\sum_{x=1}^{X_\infty} N_t(x)m(x)w(x)$, where $N_t(x)$ is the number of fish of age x at time t. Maturation at age $m(x)$ is described by a sigmoid function with 50 % maturation at $\eta_M W_\infty$. Recruitment is assumed to take place once annually and supplies the first age class with recruits. Fig. 3.1b shows the yearly surviving eggs production as a function of asymptotic size. The natural mortality for an individual is a declining function of size, $\mu(w) \propto w^{-1/3}$, which can be described in terms of the ratio between adult mortality M and the von Bertlanffy growth constant M/K as Andersen *et al.* , 2009b. The mortality for an individual because of fishing is described by a sigmoid function with inflection point at $\eta_F W_\infty$. The effect of reducing the fishing mortality on the larger individuals is examined by lowering the fishing mortality to zero for $w > \eta_{Boff} W_\infty$ (Fig. 3.1c,d). Fishery yield is determined by Baranov's catch equation (Baranov, 1918).

The ecological model is first iterated until the unfished population reaches a stable age distribution. Then, a depleted fishery is established by fishing until the spawning stock biomass is only 10 % of the SSB_{unfished}. Now, the depleted population under different scenarios has to return to safe biological levels (i.e. the SSB that can produce 95 % MSY). We estimate the time to recover (TTR) a depleted population, the changes in the SSB and the changes in the yield for 25-years period within three different recovery scenarios: (1) fishery closure, (2) lowering

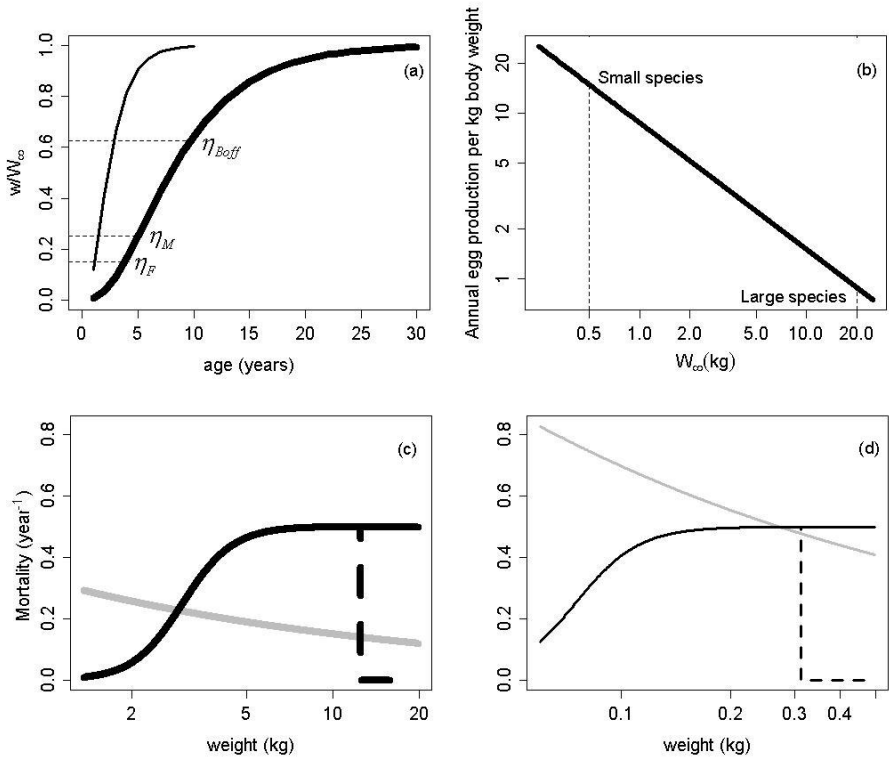

Figure 3.1: (a) von Bertalanffy growth curve, large and long-lived species (W_∞=20 kg ; thick lines) and small and short-lived species (W_∞=0.5 kg ; thin lines). (b) Annual egg production per kg body weight as a function of asymptotic size. The vertical lines are drawn at small and large species asymptotic sizes. (c) Mortality as a function of size for large and long-lived species and (d) mortality as a function of size for small and short-lived species. Grey lines are natural mortality, black lines are fishing mortality of 0.5 yr^{-1} when fishing is on all sizes larger than $\eta_F W_\infty$, and dashed lines are the fishing mortality of 0.5 yr^{-1} when fishing is on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$.

fishing mortality ($F \leq F_{MSY}$); fishing only on intermediate sizes, (3) lowering fishing mortality ($F \leq F_{MSY}$); fishing all size groups.

Thereafter, the economic desirability of the recovery plan is evaluated by a Cost Benefit Analysis (*CBA*). The analysis quantifies the costs and benefits accumulated at different points in time by translating them into a common unit: the Net Present Value (*NPV*) which is the net benefit generated by the fishery. The *NPV* for 25-years period is evaluated for the three recovery scenarios.

$$NPV = \sum_{t=1}^{T} \left(\frac{1}{1+\delta} \right)^t (Y(\rho - C_v(SSB_t)) - C_f), \tag{3.1}$$

where T=25 years, δ is the discount rate, ρ is the price per kg fish landed, C_v is the variable unit cost and C_f is the fixed cost.

We find the *NPV* by applying a discount rate (δ) of 2 % as recommended by Weitzman, 2001 for projects with medium future life (e.g. 25 years). The price (ρ) is size specific as larger fish receive a higher price. Here, we define two different prices, a low price for small fish ($w < \eta_{\text{Boff}} W_\infty$) and a double price for the larger fish ($w \geq \eta_{\text{Boff}} W_\infty$).

The variable unit cost (C_v) is the cost of fishing and it is inversely related to the *SSB*. The strength of the stock size effect is different between species of schooling and non-schooling fish. For example, it is generally assumed that there is only a weak relationship between *SSB* and variable unit cost in fisheries targeting schooling fish (Bjørndal, 1987, 1988). The reasoning behind this assumption is that because schooling fish concentrates in schools they are not uniformly distributed over an area. Once a fishing vessel has targeted a school, the catch during the harvest operation may be unaffected by the size of the fish stock. On the other hand, in non-schooling fishery the variable unit cost is assumed to be sensitive to the size of the exploited stock (Schaefer, 1957). Non-schooling fish are distributed over a wider area, if the stock size effect is present, vessels will spend less time to fill their nets when there is abundance of fish, or will return half empty in case of scarcity of fish. On the other hand, the variable unit cost does not depend on the *SSB* but on the stock that the fishing gear is seeing, that which we call the potential *SSB* (SSB_{pot}). When fishing is on all sizes $SSB_{\text{pot}} = \sum_{w=\eta_F W_\infty}^{W_\infty} SSB(w)$ but when introducing a selectivity in the upper end $SSB_{\text{pot}} = \sum_{w=\eta_F W_\infty}^{\eta_{\text{Boff}} W_\infty - 1} SSB(w)$. The cost of fishing with the selective gear (i.e. saving the larger individuals) will therefore be larger.

$$C_v(SSB_{\text{pot}}) = aSSB_{\text{pot}}^{-b}, \tag{3.2}$$

where b=1 for non-schooling, large and long-lived species and b=0.2 for schooling, small and short-lived species. The unit variable cost will be the maximum when the *SSB* is the minimum, here we assume that C_v=0.9 when the stock is depleted.

The annual fixed cost associated with all capital used in the fishery is assumed to be proportional to the fishery variable costs:

$$C_f = \gamma \cdot C_v(SSB_{10}) \cdot Y_{10} \tag{3.3}$$

where γ is the annual fixed proportion of the capital to amortize, the chosen value is based on Danish accounting statistics (Andersen *et al.* , 2009a). $C_v(SSB_{10})$ is the unit variable cost when

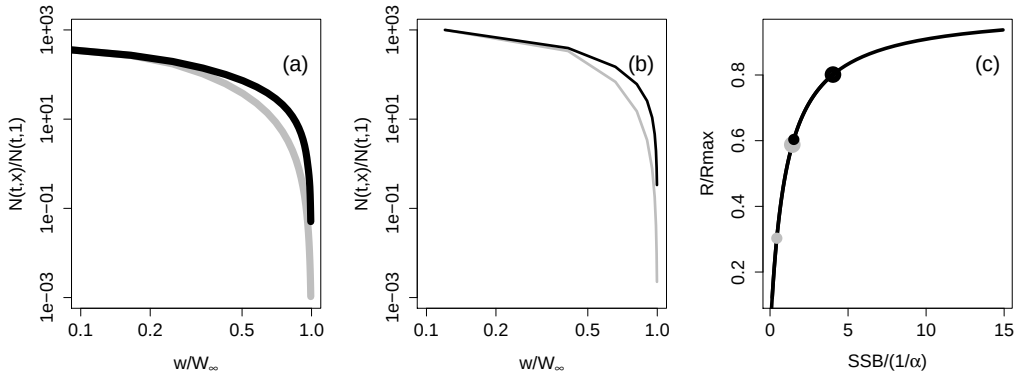

Figure 3.2: Stock structure for large and long-lived species (W_∞=20 kg; panel a) and for small and short-lived species (W_∞=0.5 kg; panel b). The spawning stock-recruit curve scaled by the maximum recruitment ($R_{\max}$) and by the value of the $1/\alpha$ to show the stable point for the large and long-lived species (big circles) and small and short-lived species (small circles) (c). Stock structure and recruitment in the recovered situation ($SSB = 95\% SSB_{\mathrm{MSY}}$; black) and in the depleted situation ($SSB = 10\% SSB_{\mathrm{unfished}}$; grey).

the SSB is 10 % SSB_{unfished} and Y_{10} is the corresponding yield.

3.3 Results

The depleted situation is created by fishing the SSB down to 10 % of the SSB_{unfished}, resulting in a depletion of the larger fish in the stock relative to the recovery situation where fishing is at F_{MSY} (Fig. 3.2a,b). The fishing mortality that leads to a depleted situation is 0.35 year^{-1} for the large species and 1.05 year^{-1} for the small species. Due to this difference in fishing mortality, the stock structure is fairly similar for both the stocks with both small and the large body size. The recruitment of the large species is higher than for the small species, both in the depleted and the recovery situations (Fig. 3.2c). This means that density dependent effects are stronger on the larger species. The relative increase in recruitment required to recover the depleted population is larger for the small species (roughly a factor two) than for the larger species (a factor of 1.3), and therefore the small species has to make a relatively larger recovery of recruitment than the large species.

The time to recover (TTR) a depleted population increases as a function of the asymptotic size (Fig. 3.3a,d). Recovery from a depleted state always takes longer for a large than for a small species. However, the difference in time is modest (6 years vs. 5 years). This is because

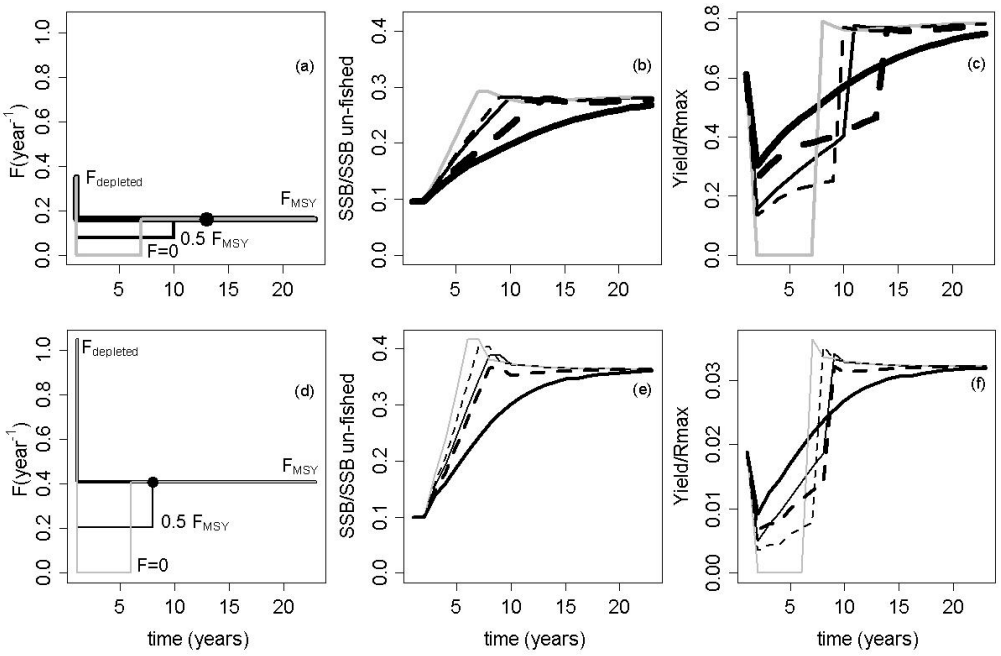

Figure 3.3: Fishing mortality (a-d), proportion of *SBB* (b-e) and yield for 25 years period (c-f) for the three strategies: fishery closure during the recovery period (grey lines), fishing mortality corresponding to *MSY* (F_{MSY}) during the recovery period (thick black lines), and fishing mortality of 0.5 F_{MSY} during the recovery period (thin black lines). Fishing on intermediate sizes until $SSB > 95\%SSB_{\mathrm{MSY}}$ (dashed lines), fishing all age groups (solid lines). Panel (a-b-c) large and long-lived species and panel (d-e-f) small and short-lived species.

of the lower impact that depletion has on the recruitment of large species than on a small species. If the recruitment has been strongly affected by reducing SSB to even lower levels, which would happen when rebuilding from a collapsed state (1 % of SSB_{unfished}), the difference between TTR for large and small species becomes more pronounced (Fig. 3.4).

For both large and small species, the shortest recovery time occurs with fishery closure during the whole recovery period (Fig. 3.3a,d). Reducing fishing pressure to F_{MSY} and removing fishing mortality on the larger fish will allow the stock to recover at a faster rate than fishing all age groups (TTR when fishing only intermediate sizes is 14 years for large species and 9 years for small species, while TTR when fishing all sizes is 23 years for large species and 14 years for small species). However, when the level of fishing pressure is 50 % F_{MSY} the difference in recovery time for both fishing all age groups and fishing only on intermediate sizes is modest

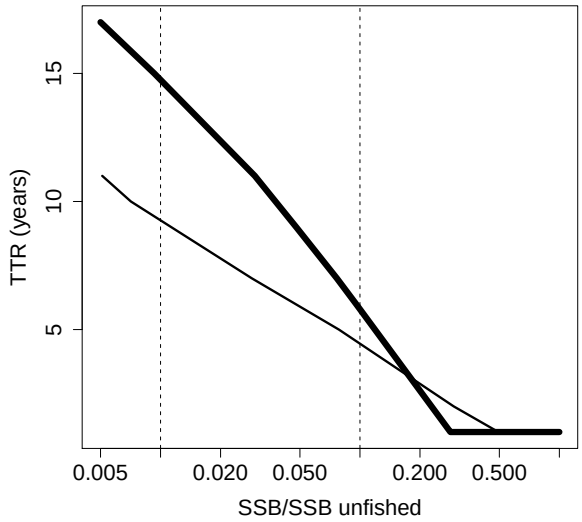

Figure 3.4: Time to recover to SSB_{MSY} as a function of the *SSB* relative to the SSB_{unfished} for the large species (thick line) and the small species (thin line). F= 0.5 yr^{-1}. The vertical dashed lines are drawn at collapsed situation (1%$\mathrm{SSB}_{\mathrm{unfished}}$) and at depleted situation (10%$\mathrm{SSB}_{\mathrm{unfished}}$).

(for large species, 9 years for both scenarios, fishing all age groups and fishing on intermediate sizes. For small species, TTR are 7 and 6 years respectively. In general, recovery scenarios that substantially restrict catches i.e. $F = 0$ or $F < 0.5F_{\mathrm{MSY}}$, during the recovery period recover populations more rapidly than those that allow higher catches during the recovery period.

The *SSB* increases constantly during the recovery phase, which indicates that both large and small species are able to recover under the three recovery scenarios (Fig. 3.3b,e). Removing fishing mortality on the larger fish during the recovery period only help to increase the *SSB* when fishing mortality rates are high (e.g. F_{MSY}).

As expected, a greater reduction in F results in a larger loss in yield in the short-term, before an increase starts at the end or after the recovery period (Fig. 3.3c,f). Thus, while more severe reductions in fishing certainly help to recover the *SSB* faster it happens at the expense of the short-term yield. When the larger individuals are not fished, the yield is distributed among the smaller size classes (from $\eta_{\mathrm{F}}W_{\infty}$ to $\eta_{\mathrm{Boff}}W_{\infty}$) so a decrease of the yield is to be expected. However, the larger bodied spawners which support reproduction are not being fished, and as a consequence the *SSB* increases faster to reach the *SSB* that produce the 95%*MSY* and an improvement of the yield will be balanced with the faster increase in the *SSB*. Adding all up,

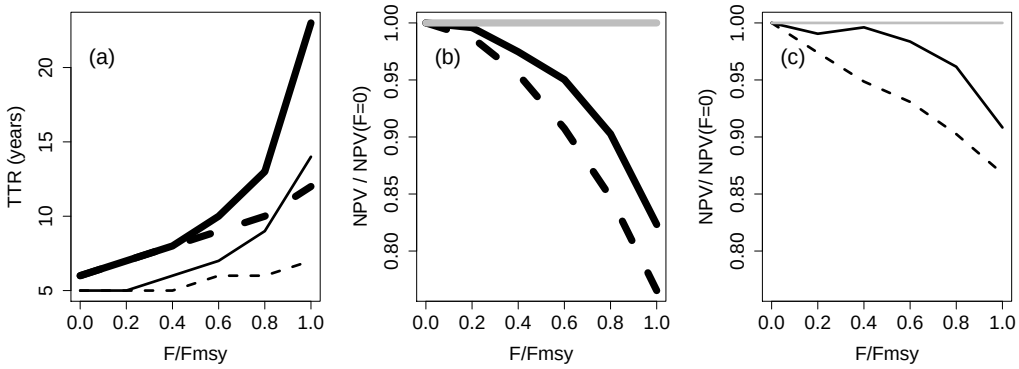

Figure 3.5: Recovery time (TTR) (a) and the net present value (NPV) for 25 years (b-c) as a function of fishing mortality relative to the F_{MSY}. Large and long-lived species (thick lines and panel b) and small and short-lived species (thin lines and panel c). Fishing on intermediate sizes during the recovery period ($SSB < SSB_{\mathrm{MSY}}$) (dashed lines), fishing on all sizes (solid black lines) and fishery closure (grey). The larger fish ($w \geq \eta_{\mathrm{Boff}} W_{\infty}$) has double price. Discount rate=2 %.

the difference between the yield fishing all size groups and fishing intermediate sizes is small for both species.

For both large and small species, all scenarios have reached recovery before or at 23 years (Fig. 3.5a). Therefore, for a comparison of the economics related with the different scenarios, the present value of the net benefit over the first 25 years is calculated. As a benchmark is chosen the fishery closure such that all economic data are presented relative to this. Setting fishing mortality to F_{MSY} will, compared with closing the fishery totally during the recovery period, for large species reduce the net benefit with between 20 and 25 % and for small species between 10 and 20 % (Fig. 3.5b,c). If fishing mortality is set to lower levels than F_{MSY}, e.g. $0.5F_{\mathrm{MSY}}$, during the recovery period, the reduction in net benefit will be less. Thus, the more catches are restricted during the recovery period ($F = 0$, $F < 0.5F_{\mathrm{MSY}}$) the more the net benefit from an economic perspective.

A sensitivity analysis of the selection of size at larger fish parameter (η_{Boff}) is addressed in Fig. 3.6. Fishing only on intermediate sizes and defining the larger fish to be smaller and younger reduce the recovery time and the reduction is larger for large species (Fig. 3.6a). As expected only the scenario when fishing is on intermediate sizes is affected by a change in the selection parameter where the NPV decreases (Fig. 3.6b,c).

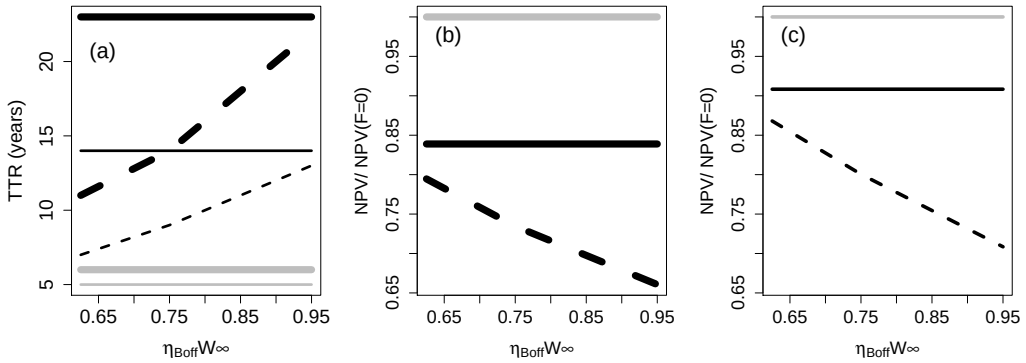

Figure 3.6: Recovery time (TTR) (a) and the net present value (NPV) for 25 years (b-c) as a function of the size of the larger fish relative to the asymptotic size. Large and long-lived species (thick lines and panel b) and small and short-lived species (thin lines and panel c). Fishing on intermediate sizes during the recovery period ($SSB < SSB_{\mathrm{MSY}}$) (dashed lines), fishing on all sizes (solid black lines) and fishery closure (grey). The larger fish ($w \geq \eta_{\mathrm{Boff}} W_\infty$) has double price. Discount rate=2 %. Fishing mortality corresponding to MSY (F_{MSY}).

3.4 Discussion

We have combined a general demographic model of exploited fish stocks with a cost-benefit analysis (*CBA*) to evaluate the ecological and economic consequences of different recovery scenarios. We emphasize that our recovery context is for moderately reduced fish populations and not those for which *SSB* has been reduced seriously to affect recruitment. The demography of the fish stock was described by a recent size/age-based framework which has the advantage that species can be described only by their asymptotic size (Andersen & Beyer, 2011). The remaining parameters are species-independent and determined by cross-species analysis of life-history invariants from the literature (Charnov, 1993). This framework makes it possible to make a general assessment of a given management action, in this case a recovery plan. The economical aspects of the recovery plan are assessed by a cost-benefit analysis that calculates the long-term net present value of the recovery plan. The cost-benefit analysis allows a quantification of the favorable and unfavorable impacts of the proposed scenarios and it has been applied to evaluate management scenarios in different fisheries (Brown & Macfadyen, 2007; Freese *et al.* , 1995; Herrick *et al.* , 1994; Kronbak *et al.* , 2009). Combining the two models made it possible to make an impact assessment of both the ecological and economical consequences of choosing one recovery plan over another of fish stocks in general.

The demographic model alone provides an ecological impact assessment of the recovery plans. The model demonstrates, not surprisingly, that small and short-lived species recover faster due to their shorter generation time (Andersen & Rice, 2010). However, the difference in TTR is modest if the stock is recovering from a depleted state. Only if the stock is completely collapsed is there a significant difference in time to rebuild. The modest difference in TTR between large and small species is somewhat counter-intuitive, and is not what is expected from simple metabolic scaling arguments (Savage *et al.* , 2004) which predict that the biological rates, and therefore also TTR, scales as weight to the power -0.25. The reason why the metabolic scaling prediction fail is because there are two competing processes going on in a fish population: the time to reach maturation and the recruitment (Andersen & Beyer, 2011), which pull TTR in opposite directions. When both processes are accounted for, the result that large species are expected to recover relatively fast from a depleted state is because their recruitment is expected to be less influenced by a 90 % reduction in SSB than a small species. Only if the stock is collapsed such that recruitment is significantly impaired, will the metabolic scaling predictions hold.

The fishing strategy that leads to the fastest recovery is the fisheries closure. However a modest fishing during the recovery does not delay the recovery significantly, in particular not for small species. Another issue that we emphasized in this paper is the contribution of the larger fish in the recovery plan. Fishing only on the intermediately sized fish, i.e. saving the larger individuals, during the recovery period did not lead to a significantly faster recovery. The importance of the larger fish was larger for large species than for small species. The saving of the larger fish only decreased the recovery time if the fishing mortality was high during the recovery period. The economical analysis also showed that the best option was to close the fishery completely during the recovery. However, the long-term losses due to a partial closure are relatively modest, and were never higher than 20 %. Saving the larger fish further reduces the NPV but the reduction is again modest, at most 25 %. In summary our results show that from narrow economic considerations based on the NPV are of minor importance in the selection of an appropriate recovery plan.

The question is then which recovery plan is the optimal seen from both an ecological and an economical perspective. The analysis clearly demonstrates that a complete closure is optimal from both perspectives. This option may, however, have other detrimental consequences not covered by the quantitative analysis performed here, e.g. socio-cultural consequences (Pollnac & Littlefielda, 1983). One immediate consequence of a fishery closure is a loss of income to

fishermen that need to seek other sources of income or state welfare. Alternatively they need to seek alternative fisheries which has other implications, e.g. it may require vessels to travel further to fish and put a higher fishing impact on other parts of the fish community. Further, industries downstream (supplier, yards) and upstream (fishing processing) can, if the referred fishery is a main supplier for the industry, be severely affected, which have additional consequences for local communities. So, even if optimal from a narrow ecological and economical perspective, there may be reasons for not recommend a complete closure of the fishery.

As the differences in *NPV* between the different recovery scenarios considered here are modest, the main constraint to consider when selecting a recovery strategy is the time to recover. As Safina *et al.* , 2005 noted, a 10 years recovery requirement is a reasonable and beneficial deadline. Our analysis demonstrated that recover within 10 years can be achieved even with a fishing mortality as high as 0.8 F_{MSY} yr^{-1} for large species and 0.9 F_{MSY} yr^{-1} for small species. Saving the the larger fish from fishing does not make an appreciable improvement in the time to recover. It has been argued that due to the inherent uncertainties in the recovery of fish stocks, delaying recovery puts the recovery of the focal stock as well as other ecosystem components at risk (Hutchings, 2000; Jackson *et al.* , 2001). On the other hand allowing a significant fishery during the recovery has many direct socio-economical and cultural benefits.

Although the model framework is a useful tool for making general predictions about the ecological and economical consequences which are relevant in a general evaluation of management strategies (Arrow *et al.* , 1996), it is a simple standard model which only describes the most important mechanisms, and which has several limitations. First of all the model framework is a single-species approach, that does not take multi-species interactions into account. Multi-species interactions affect recovery plans in at least two ways. First the ecological interactions such as competition and predation among species lead to natural variation in recruitment, survivorship, and growth of fish. However simulations with a full multi-species community model have demonstrated that the single-species model provides a good description of the recovery trajectory of that species (Andersen & Rice, 2010). The model will however not provide an assessment of the indirect effect of the recovery on the other species in the community and the potential loss of economic yield from species that are prey of the focal species (Caddy & Agnew, 2004). The other multi-species interaction is that associated with mixed-species fisheries. In some regions, many different species are captured by the same gear (e.g. many bottom trawl fisheries). Continued fishing for other species in habitats where the

depleted species is expected to recover can delay recovery (Caddy & Agnew, 2004; Murawski, 2010; Rijnsdorp *et al.* , 2007; Worm *et al.* , 2009). Consequently a recovery plan for a target depleted species which excludes measures to reduce bycatch of the depleted species (e.g. better gear selectivity, closed areas) due to fisheries for other species will likely underestimate recovery time. Our simulations implicitly assume that the simulations includes all sources of fishing mortality. Secondly, the simulations only consider a recovery of the *SSB* and not other effects, like the stock structure or the recovery of certain phenotypes or genotypes of the stock (Petitgas *et al.* , 2010). Still, a recovery of the *SSB* is often a good proxy for the recovery of other aspects of a stock as well. All taken together, the simulations should be used a rule-of-thumb guideline for how different species and recovery plans are expected to affect the recovery of a stock.

In our simulations we have paid particular attention to the larger fish, but we have disregarded maternal effects, which may increase the importance of the larger fish. We have chosen not to include maternal effects explicitly, partly because they are difficult to quantify, and partly because in our second chapter we have shown that maternal effects have a limited impact on the reproductive ability of the whole stock. The parameters for both the demographic and the economical models have been set at reasonable average values, but there may be large variations between stocks. Therefore the results should be regarded as indicative but not prescriptive for specific stocks or circumstances. If the model is to be applied in for a stock where one aspect of either its ecology, e.g. high natural mortality or significant maternal effects, or economic importance, e.g. exceptionally large price difference between different sizes, a simulation may need to be carried out using specific stock-specific parameter values.

In conclusion, the economic analysis in this paper indicates that the differences between choosing one recovery scenario over the other are limited. There are differences in the recovery time between scenarios, but some fishing mortality may be allowed if the recovery should be completed only in 10 years. The larger fish does not matter much neither from an economic nor from an ecological perspective. Only if there is a high fishing pressure during the recovery period can saving the larger fish reduce recovery time significantly.

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Table 3.1: Model equations

Process	Equation	Number
Von Bertalanffy growth equation[a]	$w(x) = W_\infty(1-e^{-Kx})^3$	(1)
Natural mortality[b]	$\mu(x) = \frac{1}{3}\hbar\eta_M^{1/3}\left(\frac{M}{K}\right)w(x)^{-1/3}$	(2)
Fishery Yield[c]	$Y = \sum_{x=1}^{X_\infty} B(x)F(x)\frac{1-e^{-(\mu(x)+F(x))\Delta t}}{(\mu(x)+F(x))\Delta t}$	(3)
Population equation	$N(t,x) = N(t-1,x-1)e^{-(\mu(x)+F(x))\Delta t}$	(4)
Recruitment equation[d]	$R(SSB) = \frac{\alpha SSB}{(1+\alpha SSB)R_{max}}$	(5)

[a] Bertalanffy, 1938
[b] Andersen *et al.* , 2009b
[c] Baranov, 1918
[d] Beverton & Holt, 1957

Table 3.2: Model parameters

Symbol	Parameter	Value
Control parameters:		
F	Fishing mortality	free (0,...,2 yr^{-1})
W_∞	Asymptotic (maximum) weight	free (0.5kg, 20kg)
X_∞	Maximum age	free (10years, 30years)
Fundamental parameters:		
$\hbar$	Growth constant[a]	16.2 $g^{1/3}$ yr^{-1}
M/K	Mortality/growth relation[b]	0.95
η_M	Ratio between size at maturation and W_∞[c]	0.25
η_F	Ratio between size at 50 % F and W_∞	0.15
η_{Boff}	Ratio between size of the largest individuals and W_∞	0.625
Δt	Time scale	1 year
R_{max}	Maximum rate of recruitment at high stock biomass	-
α_0	Constant in recruitment equation[d]	$6{\cdot}10^4 yr^{-1}$
Derived parameters:		
K	von Bertalanffy growth constant	$\hbar W_\infty^{-1/3}/3$
α	Productivity parameter of the stock recruitment equation [d]	$\alpha_0(\frac{W_\infty}{0.01})^{-2.3/3}$

[a] At 10° (Andersen *et al.* , 2008)

[b] Andersen *et al.* , 2009b

[c] See Beverton, 1992

[d] Hall *et al.* , 2006

Chapter 4

Can size-based management regulations minimize the evolutionary changes caused by fishing?

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Abstract

There is increasing evidence that intense size-selective fishing may cause evolutionary changes in life-history traits of exploited fish stocks, which has led to a call for management which minimizes unwanted evolutionary changes. Here, we make a quantitative assessment of the potential evolutionary benefits of imposing an maximum size-limit for fishing on a stock and the consequent changes in yield. This is achieved by calculating the expected selection response on three life-history traits: size at maturation, growth rate, and reproductive investment under two different fishing scenarios, with and without a maximum-size limit. We find that each life-history trait responds differently to the introduction of size-selective fishing regulations, and that only a reduction in fishing mortality will reduce the magnitude of the selection response on all traits. Specifically, an upper size limit will mitigate fishing-induced evolution on some traits (e.g. size at maturation) but not on others (e.g. growth and reproductive investment). The consequent changes in fisheries yields are less than 10 % per decade. We conclude that size-based management regulations alone are unable to mitigate fisheries induced evolution on all evolving traits.

Key words: fisheries-induced evolution, fisheries management, quantitative genetics

4.1 Introduction

Fisheries induced evolution have recently received considerable attention in the literature (reviewed by Conover & Baumann, 2009; Dunlop *et al.* , 2009; Hutchings & Fraser, 2008; Jørgensen *et al.* , 2007; Kuparinen & Merilä, 2007). In particular, fishing may cause evolutionary changes in life-history traits, such as age and size at maturation (Andersen *et al.* , 2007; Ernande *et al.* , 2004; Grift *et al.* , 2003; Rijnsdorp, 1993; Trippel, 1995), changes in growth (Ricker, 1981; Swain *et al.* , 2007; Williams & Shertzer, 2005) or reproductive investment (Arlinghaus *et al.* , 2009; Rijnsdorp *et al.* , 2005). Other studies have expanded further by focusing on the evolution of multiple traits (Andersen & Brander, 2009; Matsumura *et al.* , 2011; Rijnsdorp, 1993; Walsh *et al.* , 2006; Wang & Hook, 2009). These life-history traits determine the age and size composition of a stock and the stock's reproductive potential and therefore, changes in these life-history traits have important consequences for population dynamics (Bronikowski *et al.* , 2002; Shertzer & Ellner, 2002) and, consequently, yield from fishery (Conover & Munch, 2002; Heino, 1998; Jørgensen *et al.* , 2007; Law, 2000; Law &

Grey, 1989; Ratner & Lande, 2001) as well as the capacity for population recovery (Enberg *et al.* , 2009; Hutchings, 2005; Walsh *et al.* , 2006). All these studies highlight the need to incorporate the evolutionary responses to fishing to ensure the best scientific advice for fishery management.

It is well known that the two main forces affecting the rate of evolution in an exploited fish stock are: the intense fishing mortality (Barot *et al.* , 2004; Ernande *et al.* , 2004; Grift *et al.* , 2003; Law & Grey, 1989; Olsen *et al.* , 2004; Rijnsdorp, 1993; Sharpe & Hendry, 2009) and its size-selective nature which, mainly target large individuals (the "Big old fecund fish" (Boff)) (Conover & Munch, 2002; Darimont *et al.* , 2009; Law, 2007; Ricker, 1981; Walsh *et al.* , 2006). High fishing pressure on large individuals induces an evolution to earlier maturation, decreased body size, and increased investment in reproduction (Andersen & Brander, 2009). It has been suggested that the maintenance of the largest individuals in a population by applying a maximum size-limit will diminish the evolutionary consequences of fishing (Conover & Munch, 2002; Law, 2007), particularly because of the contribution of the large individuals to the total reproductive output of the population (Birkeland & Dayton, 2005).

Reducing fishing mortality will reduce the rate of evolution, but so far only few studies have explored the evolutionary benefits of applying a maximum size-limit relative to other management strategies (Baskett *et al.* , 2005; Jørgensen *et al.* , 2009; Matsumura *et al.* , 2011; Wang & Hook, 2009; Williams & Shertzer, 2005). The goal of this article is to make a quantitative assessment of the potential evolutionary benefits of saving the largest individuals in a population. The effects are estimated for the impact on the expected rates of fisheries-induced evolution for three different life-history traits – size at maturation, growth rate and reproductive investment – and the consequent changes in the yield. The questions addressed here are: Can a particular choice of size-selective fishing minimize the consequences of fisheries-induced evolutionary changes in all three life-history traits? And: how does the fishery yield change from this evolutionary response? Within this comparative framework, we attempt to evaluate the capability of the largest individuals to mitigate the evolutionary change, while also maintaining a sustainable annual yield.

We use a published size and life-history based model (Andersen & Brander, 2009; Andersen *et al.* , 2007) to calculate the expected selection responses induced by fishing mortality and its size-selective and the expected impact in the yield for a given stock. The model is general and uses life-history parameters based on a characterization of a fish stock by the asymptotic weight (W_∞) and the ratio between adult mortality and von Bertalanffy growth rate M/K. The

analysis in this paper is on two theoretical stocks with life history traits typical of a large and long-lived species ($W_\infty = 20$ kg) and of a small and short-lived species ($W_\infty = 0.5$ kg).

4.2 Methods

The expected evolutionary response to fishing is calculated by combining standard demographic analysis with quantitative genetics. The trade-offs involved enter the calculation through the equations describing growth and mortality using size-based parameterizations of rates (Andersen *et al.* , 2007).

The selection response r_ϕ of a trait ϕ is calculated by the linearized Breeders' equation from the life-time expected reproductive output R_0 as a function of the trait (ϕ) (Andersen *et al.* , 2007):

$$r_\phi = h^2 \sigma_\phi^2 \left. \frac{R_0'}{R_0} \right|_\phi , \tag{4.1}$$

where h^2 is the heritability of the trait, σ_ϕ is the width of the distribution of the trait in the population, R_0' is the derivative of the lifetime reproductive output R_0 with respect to the trait evaluated at the current value of the trait ϕ. The rate of evolution of a trait due to an external perturbation, here fishing, is calculated as the differential selection response, which is the difference between the selection responses with fishing $r(F)$ and without fishing mortality $r(F=0)$. The differential selection response is transformed from units of "per generation" to per year by dividing with the expected age of maturation (used as a proxy for generation time) T and normalized by the trait value: $(r(F) - r(F=0))/(\phi T)$. The differential selection response (from now on referred to as the "selection response") is therefore a measure of the expected evolutionary change per year.

The traits considered in this analysis are: size at maturation ϕ_m, consumption rate ϕ_h, and reproduction investment ϕ_k. For each trait there are associated trade-offs specifying how a change in the trait influences growth and mortality (Andersen & Brander, 2009). The trade-off emerges naturally from a mass-balance of the energy allocation within an individual. ϕ_m: the earlier maturation, the more secure is the individual of reproducing, however earlier maturation means forgoing potential growth, leading to an even larger reproductive output. ϕ_h: increased consumption leads to faster growth and reproduction but also incurs an increased risk of predation mortality, due to more time spent foraging while exposed to predators. ϕ_k: increased investment into reproduction leads to a higher reproductive output, but lower growth.

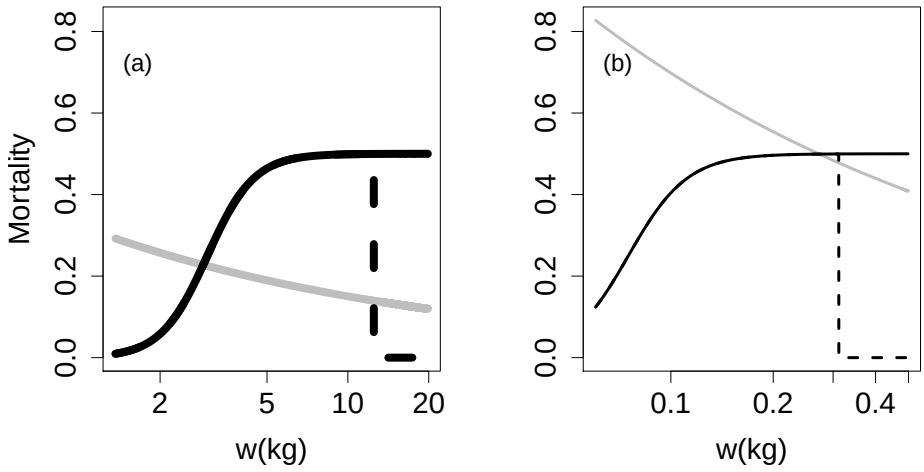

Figure 4.1: Mortality as a function of size for large and long-lived species (a) and small and short-lived species (b). Grey lines are natural mortality, solid black lines are fishing mortality of $F = 0.5$ yr^{-1}, and dashed black lines are fishing mortality of $F = 0.5$ yr^{-1} when the maximum size-limit ($w > \eta_{\text{Boff}} W_\infty$) is imposed.

In practical terms the traits ϕ are non-dimensional constants with a default value of 1, which influence the life-history parameters in the growth and mortality equations: size at maturation m, growth constant $\hbar$, and mass-specific egg production k_r. The other parameters in the model are mostly non-dimensional life-history constants (Charnov, 1993) for which expected values can be found from cross-species analyses (Andersen & Beyer, 2011) . In this manner a large part of the variation between fish stocks is related to the the trait asymptotic size W_∞ (or, equivalently, size at maturation). The equations required to calculate fitness $R_0(\phi)$, growth $g(w)$, and generation time T are given in Table 4.1, (1-3).

Natural mortality for an individual is a declining function of size, $\mu(w) = a\hbar w^{n-1}$ and fishing mortality is given by a sigmoid function with inflection point at size $\eta_{\text{F}} W_\infty$. We consider two different types of size-selective mortality across variable levels of fishing mortality: (i) without a maximum-size limit (i.e. fishing on all individuals above a minimum size η_{F}) and (ii) with a maximum size-limit where the immature and the large individuals escape simultaneously (i.e. fishing is on fish of intermediate sizes $\eta_{\text{F}} < w < \eta_{\text{Boff}}$) (Fig. 4.1a,b).

The relative yield is determined by multiplying the yield per recruit with the recruitment. This calculation therefore goes beyond the calculation of yield by Andersen & Brander, 2009

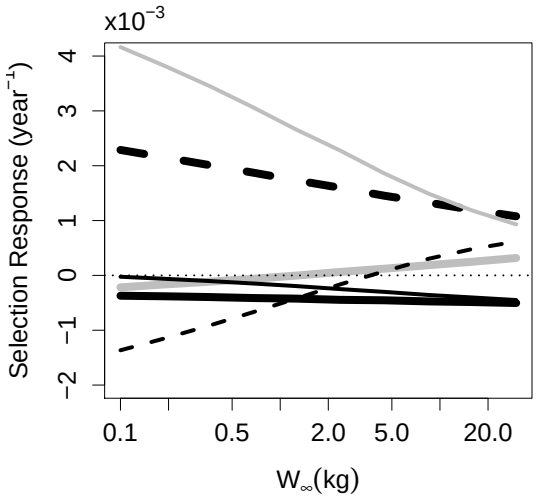

Figure 4.2: Expected selection response due to fishing $F = 0.5$ yr^{-1} for changes in size at maturation (solid black lines), growth rate (grey lines) and investment in reproduction (dashed black lines) as a function of asymptotic size. Fishing is on all sizes larger than $\eta_F W_\infty$ (i.e. without a maximum-size limit; thick lines) and fishing is on intermediate sizes (i.e. with a maximum-size limit $\eta_F < w/W_\infty < \eta_{Boff}$; thin lines).

who assumed a constant recruitment. The recruitment is specified by a Beverton-Holt recruitment function:

$$R = R_{\max} \frac{R_p}{R_{\max} + R_p} \tag{4.2}$$

where $R_{\max}$ is the maximum rate of recruitment at high stock biomass, and the egg production R_p is calculated by multiplying the individual-level investment into reproduction $\phi_k \hbar (m/\eta_M)^{n-1} w$ the population size. The calculation of the population size at equilibrium follows the procedure in Andersen & Beyer, 2011, see Table 4.1, (4-6).

4.3 Results

In general, we have found the same trend in the expected selection responses as Andersen & Brander, 2009, but the exact values differ because we have used an updated set of parameters from Andersen & Beyer, 2011 (Fig. 4.2, thick lines). The selection response of size at maturation ϕ_m is always negative, indicating that fishing creates a selection pressure towards a reduction of the size at maturation. The selection response of growth is small compared to

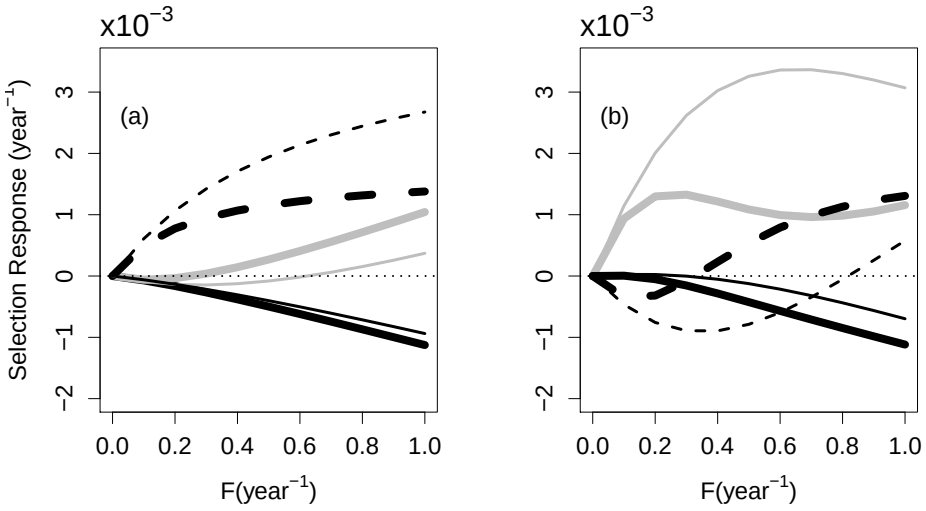

Figure 4.3: Expected selection response for changes in size at maturation (solid black lines), growth rate (grey lines) and investment in reproduction (dashed black lines) as a function of fishing mortality. (a) Fishing is on all sizes larger than $\eta_F W_\infty$ (i.e. without a maximum-size limit) and (b) fishing is on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$ (i.e. with a maximum-size limit). Small species (W_∞=0.5 kg; thin lines) and large species (W_∞=20 kg; thick lines).

the other traits, and vary from negative on small fish species to positive on large species. The selection response of investment in reproduction ϕ_k has the largest selection response. It is always positive and decreases with asymptotic size. The trade-off between investment into reproduction and growth is evident as the selection responses of these two traits vary inversely with asymptotic size. The selection responses are generally increasing as fishing is intensified (Fig. 4.3a), except for the investment into growth that is negative for small fishing mortalities and positive for large fishing mortalities. This is due to the trade-off between growth and predation mortality which increases predation mortality with growth. At high fishing mortalitity, the impact of predation mortality is less significant, and the selection response on growth changes sign and becomes positive.

The introduction of an upper size limit creates a size refuge for large individuals. This makes it more favorable to forego investment into reproduction to be able to grow quickly through the size window where fishing operates (Fig. 4.2, thin lines). This is evident through a large increase in growth and a much reduced selection response in investment into gonads. The impact of introducing the size refuge is largest for small fish species. The impact of

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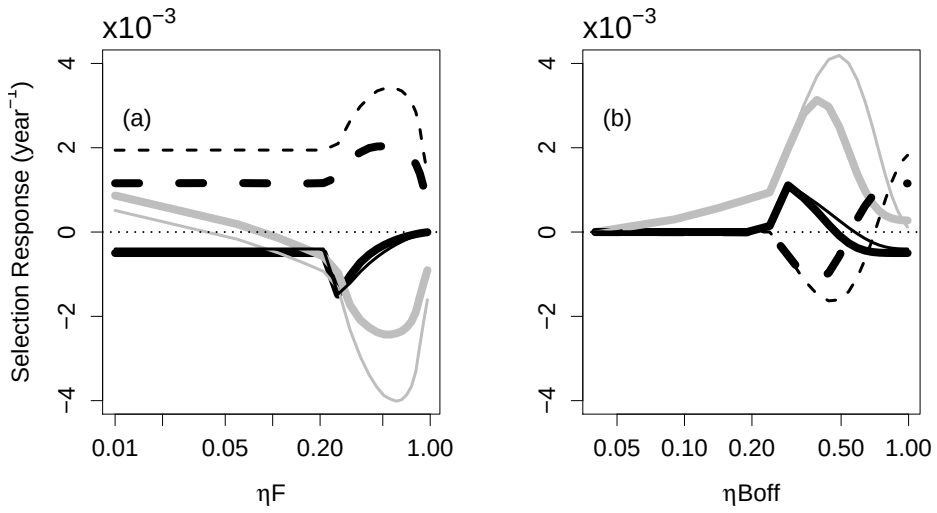

Figure 4.4: The impact of changing the minimum size-limit η_F (a) and the maximum size-limit η_{Boff} (b) on the rates of evolution of size at maturation (solid black lines), growth rate (grey lines) and investment in reproduction (dashed black lines). (a) $F = 0.5$ yr^{-1} and fishing is on all sizes larger than $\eta_F W_\infty$ (i.e. without a maximum size-limit). (b) $F = 0.5$ yr^{-1}, fishing is on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$ and the minimum size-limit is η_F=0.05. Small species (W_∞=0.5 kg; thin lines) and large species (W_∞=20 kg; thick lines).

changing the fishing mortality has a similar effect as without the size refuge (Fig. 4.3b), but the interplay between investment into growth and reproduction is more complex. Even for small fishing intensity investment into growth is increasing sharply at the expense of investment into reproduction. This investment pays off because it makes it more likely to reach the size refuge where overall mortality is low. At large fishing mortalities the investment into reproduction is increasing, similar to the effect without the size refuge.

To understand the impact of size-selective regulation on the mitigation of selection responses of the traits in more detail, we examine the effects of changing the minimum η_F and the maximum-size limit η_{Boff} for both small and large species (Fig. 4.4). When fishing starts much before size at maturation faster growth is favored to be able to reach the size at maturation before being caught by fishing. However, if a fish mature before they are fished, slower growth and increased investment in reproduction is favored, because this ensures more reproduction before the size at which fishing starts is reached. Lowering the upper size limit below the size at maturation makes the induced selection responses on investment into reproduction and size

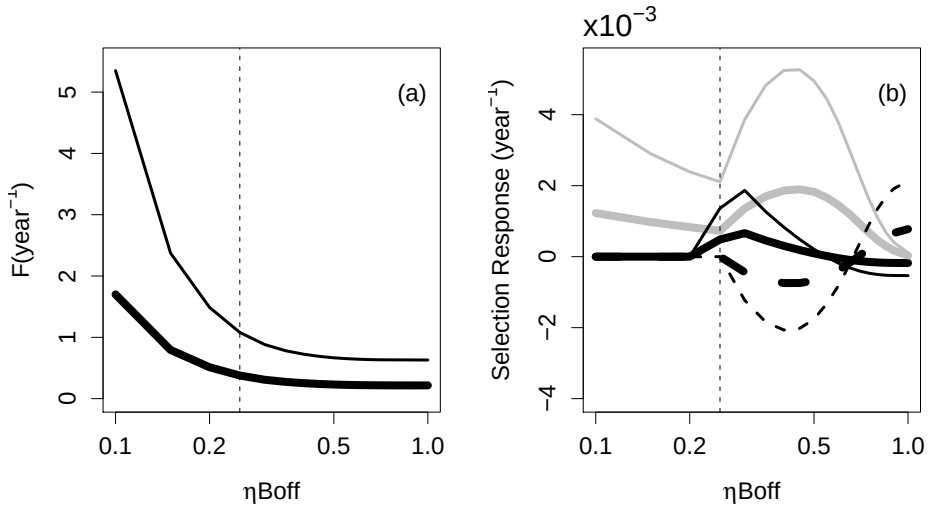

Figure 4.5: The impact of changing the maximum size-limit η_{Boff} on fishing mortality (a) and on the rates of evolution of size at maturation (solid black lines), growth rate (grey lines) and investment in reproduction (dashed black lines) (b). Fishing is on intermediate sizes $\eta_{\text{F}} < w/W_\infty < \eta_{\text{Boff}}$ and the minimum size-limit is η_{F}=0.05. The vertical dashed lines are drawn at the ratio between size at maturation and $W_\infty(\eta_{\text{M}}$=0.25). Small species (W_∞=0.5 kg; thin lines) and large species (W_∞=20 kg; thick lines).

at maturation to almost zero, and leads to a very small selection response on growth. Fishing only on immature fish is therefore the only size-selection management strategy that lowers the selection response on all traits simultaneously.

The reduction in evolutionary rates resulting from the upper size limit comes as a cost in term of lower yield. To explore the possibility of mitigating that cost, we examine the effects of changing the maximum-size limit η_{Boff} adjusting the fishing mortality such that the yield is kept constant (Fig. 4.5a). As long as the upper size limit is larger than the size at maturation, the fishing mortality does not need to increase appreciably to keep the fishery yield constant. However, as the upper size limit is decreased below the size at maturation, fishing mortality has to increase considerably to maintain the same yield for both small and large species. The result in terms of evolutionary rates is that they increase correspondingly, such that the selection responses on growth and investment in reproduction are on the same order of magnitude as without the upper size limit (Fig. 4.5b).

The expected relative changes in yield due to changes in the traits as a function of asymp-

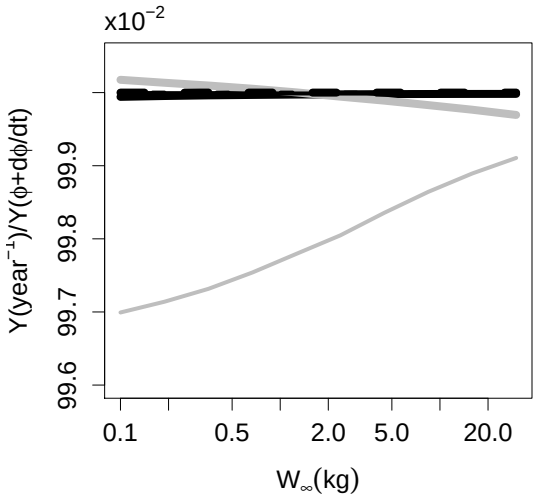

Figure 4.6: Expected relative change in yield given changes in size at maturation (solid black lines), growth (grey lines) and investment in reproduction (dashed black lines) as a function of asymptotic size. Fishing, $F = 0.5$ yr^{-1}, is on all sizes larger than $\eta_F W_\infty$ (i.e. without a maximum-size limit; thick lines) and fishing, $F = 0.5$ yr^{-1}, is on intermediate sizes $\eta_F < w/W_\infty < \eta_{Boff}$ (i.e. with a maximum size-limit; thin lines).

totic size are shown in Fig. 4.6. A small change in yield is only given by a selection response of growth when fishing is on all sizes larger than $\eta_F W_\infty$ and for the smallest species.

4.4 Discussion

We have extended the model by Andersen & Brander, 2009 to quantify the potential evolutionary benefits of saving the large individuals on three life-history traits: size at maturation, growth and reproductive investment and the consequent changes in yield. While most of the quantitative-genetic models developed to evaluate selective pressures on fish populations are species-specific (e.g. cod (*Gadus morhua*), northern pike (*Esox lucius*), red snapper (*Lutjanus campechanus*), rockfish (*Sebastes paucispinis* and *S. ruberrimus*)) the model used here is based on life history invariants and it can therefore be applied to gain general insights which are not limited to specific stocks.

Increasing the minimum size-limit is one of the most common harvest regulations in commercial fisheries, and it is usually suggested that the minimum size-limit should be as large

as possible. However, an introduction of a maximum size-limit has been suggested as an alternative to a minimum size-limit to reduce the strength of the expected selection response to fishing mortality (Conover & Munch, 2002; Law, 2007). It seems reasonable to assume that a maximum size-limit will mitigate fisheries induced evolution on the evolving life-history traits. Confirming this expectation, we found that the selection response of size at maturation was reduced through a maximum size-limit only for small species and the reduction was larger with higher fishing pressure. However, under stricter regulations (i.e. $\eta_{\text{Boff}} < 0.5$), the response becomes even positive for both large and small species. These results are consistent with previous studies that suggested that the magnitude of the selection reponse of size at maturation of commercial fish decrease as regulation become stricter (for bocaccio (*Sebastes paucispinis*) Baskett *et al.* , 2005, for Northeast Arctic cod (*Gadus morhua*) Jørgensen *et al.* , 2009 and for Northern pike (*Esox lucius*) Matsumura *et al.* , 2011).

On the other hand, an introduction of a maximum size-limit did not mitigate the expected selection response of the other two traits (growth and investment in reproduction) as they responded differently to the introduction of this upper size limit. Our results on the expected selection response of growth show that an introduction of a maximum size-limit will favour a faster growth rate for all fish stocks, such that they increase the chance of avoiding fishing by growing into the larger size-refuge. The strength of selection response is larger for small species than for large species and the largest response is at moderate to high fishing mortality for both species. However, by applying a high maximum size-limit (i.e. $\eta_{\text{Boff}} > 0.5$) the larger size-refuge ($w \geq \eta_{\text{Boff}} W_\infty$) is practically unreachable and the expected selection response of growth decrease. Thus, under a large maximum size-limit, the optimal solution is to invest less in growth and to increase the investment in reproduction to assure a successful spawning event. In agreement with our study, Hilborn & Minte-Vera, 2008 found for cod-like species, a small evolutionary impact on growth without size-selective regulation and Matsumura *et al.* , 2011 found that establishing a maximum size-limit increase the strength of selection on growth for northern pike.

Our results show changes in the direction on the expected selection response of reproductive investment when a maximum size-limit is applied. The selection response becomes negative and strong for small species however, it is positive and weaker for large species. Intense fishing mortality makes the respond positive for both species. It seems clear that the direction of selection on reproductive investment depends not only on the size-selective fishing, but also on the fishing pressure. While the selection response of growth and reproductive investment

evolve independently, we observe that changes in one trait influence the evolution of the other, such that evolution of these traits are not entirely independent. Along these lines, we observe that evolution of growth and reproductive investment tended to compensate each other.

About the consequences of the evolutionary changes in all three life-history traits on the fishery yield, only the positive response on growth, with the incorporation of a maximum size-limit, had a negative effect on the yield for small species. Some studies have already attempted to analyze yield changes resulting from fishing-induced evolution, and most of them predicted yield to decline (Heino, 1998; Law & Grey, 1989; Okamoto *et al.* , 2009). Also a laboratory experiments by Conover & Munch, 2002 have demonstrated a declining yield in response to size-selective exploitation.

The general conclusion is that the introduction of size-refuge for large fish, while beneficial for some traits, will not be beneficial for all traits at once. Even if such a management measure might be practically possible, it is therefore not a solution to minimize unwanted evolutionary changes in harvested fish populations. The only possible size-selection management option to minimize evolutionary changes on all traits seems to let the maximum size-limit be *below* the size at maturation, effectively only catching immature fish, and banning fishing on mature fish altogether. Such a management measure is in line with the recent proposal of "balanced" fishing selection patterns with a higher fishing mortality on smaller individuals than on larger individuals (Zhou *et al.* , 2010). It is important to realize that this reduction in evolutionary rates comes at a cost of a lowered yield. If the yield is to be maintained fishing mortality should be increased correspondingly, and consequently the introduction of size-refuge for large fish will not reduce fishery-induced selection responses. We therefore conclude that there are no silver-bullet in terms of size-based fishing patterns which will reduce unwanted evolutionary effects of fishing – the only safe remedy is a reduction in fishing effort.

Table 4.1: Model equations

Process	Equation	Number
Fitness	$R_0(\phi) = p_{w_0 \to m} \int_m^{\widetilde{W}_\infty} p_{m \to w} \frac{\phi_k k r}{g(w)} dw$	(1)
Growth	$g(w) = \phi_h \hbar w^n - [\varepsilon_r + \phi_k(1 - \varepsilon_r) H(w - \phi_m m)] \hbar (m/\eta_M)^{n-1} w$	(2)
Generation time	$T = \frac{1}{\hbar(n-1)} W_\infty^{1-n} ln(1 - \eta_M^{1-n})$	(3)
Relative size distribution	$\frac{N}{R} = \hbar^{-1} w_0^{a-1} w^{-n-a} \left[1 - \left(\frac{w}{W_\infty}\right)^{1-n}\right]^{\frac{a}{1-n}-1}$	(4)
Relative SSB	$\frac{B}{R} = \int_{w_0}^{W_\infty} \psi_M(w) \frac{N_w}{R} w \, \mathrm{d}w$	(5)
Relative recruitment	$\frac{R}{R_{max}} = \left(1 - \frac{W_\infty^{1-n}}{\varepsilon_r \phi_k \hbar B/R}\right)$	(6)

Table 4.2: Model parameters

Symbol	Parameter	Value
Control parameters:		
F	Fishing mortality	free
W_∞	Asymptotic size	0.5 and 20 kg
w_0	Starting size	free
w	Individual weight	
Life-history parameters:		
$R_{\max}$	The maximum rate of recruitment	
$\hbar$	Growth constant[a]	6.41 g^{1-n} yr^{-1}
n	Exponent for consumption [a]	3/4
h^2	Heritability	0.2
σ	Coefficent of variation traits	0.2
η_M	Ratio between size at maturation and W_∞ [b]	0.25
η_{F}	Ratio between size at 50 % F and W_∞	0.15
η_{Boff}	Ratio between size of the largest individuals and W_∞	0.625
a	Physiological mortality[a,c]	0.35
ε_{r}	Recruitment efficiency[a]	0.2
u_M, u_F, u_B	Width parameters for step functions	10
ϕ_m, ϕ_h, ϕ_k	Evolutionary traits: size at maturation, growth and reproduction investment	
Derived parameters:		
m	Size at maturation	$\eta_M W_\infty$
k_{r}	Mass-specific egg production[d]	$\varepsilon_{\mathrm{r}} \hbar W_\infty^{n-1} w$
$p_{w_1 \to w_2}$	Probability of surviving from size w_1 to w_2	$\exp\left[-\int_{w_1}^{w_2} \mu(w)/g(w) dw\right]$
$\widetilde{W}_\infty$	The realized maximum size	$[(\delta + \phi_k k r/w)/(\phi_h \hbar)]^{1/(n-1)}$
$\psi_{\mathrm{M}}(w)$	Fraction of mature individuals at a given size	$\left[1 + \left(\frac{w}{\eta_{\mathrm{M}} W_\infty}\right)^{-u_M}\right]^{-1}$
$\psi_{\mathrm{F}}(w)$	Fraction of individuals reaching the size $\eta_{\mathrm{F}} W_\infty$	$\left[1 + \left(\frac{w}{\eta_{\mathrm{F}} W_\infty}\right)^{-u_F}\right]^{-1}$
$\psi_{\mathrm{B}}(w)$	Fraction of individuals reaching the size $\eta_{\mathrm{Boff}} W_\infty$	$\left[1 + \left(\frac{w}{\eta_{\mathrm{Boff}} W_\infty}\right)^{-u_B}\right]^{-1}$

[a] See Andersen & Beyer, 2011

[b] See Beverton, 1992

[c] The value of a is determined from its relation to the M/K life history invariant (Andersen *et al.* , 2007)

[d] The egg-production of an individual is assumed to be proportional to the allocation to reproduction

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Glossary

Big Old Fecund Fish (Boff): are the larger, older females which, according to recent research results, produce more eggs in each spawning event than smaller-younger females do. Additionally, the eggs of larger females are often healthier and more likely to survive. Older fish are more likely to survive and contribute in the bad years when environmental factors mean reduced recruitment to the fish stocks.

Collapsed Stock ($\mathbf{SSB}_1$) : a stock driven by fishing to very low level of abundance compared to historical levels (e.g. SSB <1 % SSBunfished), with dramatically reduced spawning stock biomass and consequently the reproductive capacity. It requires rebuilding plans.

Cost Benefit Analysis (CBA): the analysis that quantifies the costs and benefits accumulated at different points in time by translating them into a common unit: the Net Present Value (NPV) which is the net benefit generated by the fishery. Here, the economic desirability of a recovery plan is evaluated by a Cost Benefit Analysis.

Depleted Stock ($\mathbf{SSB}_{10}$) : a stock driven by fishing to low level of abundance compared to historical levels (e.g. SSB <10 % SSBunfished), whose spawning stock biomass has been lowered such that it produces a lower yield from the fishery than it potentially could, but whose recruitment is not necessarily substantially limited by the spawning stock biomass. It requires particularly recovery plans.

$\mathbf{F}_{10}$: the fishing mortality rate that reduces the spawning stock biomass (SSB) to 10% of the $\mathrm{SSB}_{unfished}$.

$\mathbf{F}_1$: the fishing mortality rate that reduces the spawning stock biomass (SSB) to 1% of the $\mathrm{SSB}_{unfished}$.

$\mathbf{F}_{crash}$: fishing mortality rate corresponding to very high value of fishing. A stock fished at or above this level for a prolonged period of time is expected to collapse.

$\mathbf{F}_{MSY}$: the fishing mortality rate that produces the maximum sustainable yield (MSY). Used as a fisheries reference point, F_{MSY} is the implicit fishing mortality target of

many regional and national fishery management authorities and organizations.

Fisheries Reference Points: specific values for the variables that describe the state of a fishery system which are used to evaluate its status. Reference points are most often specified in terms of fishing mortality rate and/or spawning stock biomass. These may indicate (a) a desired state of the fishery, such as a fishing mortality rate that will achieve a high level of sustainable yield, or (b) a state of the fishery that should be avoided, such as a high fishing mortality rate which risks a stock collapse and long-term loss of potential yield. The former are referred to as target reference points, and the latter are referred to as limit reference points or thresholds. Some common examples are F_{crash}, F_{10}, and F_{MSY}.

Fishing Mortality (F): death or removal of fish from a population due to fishing, usually expressed as the annual mortality, the percentage of fish dying in one year, or the instantaneous rate F, and which can range from 0 for no fishing to very high values such as 1.5 or 2 (this is possible with short-lived, fast growing species such as anchovies).

Generation Time (T): is the expected time to reach maturation.

Growth Rate (K): the increase in weight of a fish per year (or season), divided by the initial weight. In fish this is often measured in terms of the parameter K of the von Bertalanffy curve for the mean weight as a function of age.

Maternal effects (ϕ): refer to the particular phenomenon in which larger and older females produce eggs of higher quality in terms of survival han the eggs from smaller-younger females.

Maximum age ($\mathbf{X}_\infty$) : the maximum expected age, on average, for a species, cohort, stock, or a population in the absence of fi shing or human-induced mortality.

Maximum Sustainable Yield (MSY): the largest average catch or yield that can continuously be taken from a stock under existing environmental conditions.

Natural Mortality (μ): natural mortality in fish is a declining function of size. The main cause of natural mortality is predation and cannibalism, in this thesis we did not include senescence.

Net Present Value (NPV): the value of an enterprise at the present time, after applying the process of discounting its costs and benefits.

Population Dynamics: the study of fish populations and how fishing mortality, growth, recruitment, and natural mortality affect them.

Population: the number of individuals of a particular species that live within a defined area (see *Stock*).

Rebuilding: implementing management measures that increase a collapsed fish stock to its target size (e.g. SSB_{MSY}).

Recovering: implementing management measures that increase a depleted fish stock to its target size (e.g. SSB_{MSY}).

Recruitment(R): the number of young fish that survive (from birth) to age 1 or grow to a specific size.

School: aggregation of fish that move together as a group. It is usually considered that schooling reduces the impact of predation. Schools can be themselves aggregated in concentrations.

Selection response: is a measure of the expected evolutionary change due to an external perturbation, here fishing, per year.

Single-Species Model: a model describing the dynamics of a species that does not explicitly incorporate the effects of interactions with other species.

Size Limit: a minimum or maximum limit on the size of fi sh that may be legally be caught.

Spawning Stock Biomass (SSB): the total weight of all fish (both males and females) in the population that contribute to reproduction. Defined as the biomass of all individuals beyond age or size at first maturity i.e. beyond the age or size class in which 50 percent of the individuals are mature.

SSB_{MSY} : the long-term average biomass that would be achieved if fishing at a constant fishing mortality rate equal to F_{MSY}.

$\text{SSB}_{unfished}$: unfished biomass, using mathematical models, it is generally calculated as the long-term average biomass value expected in the absence of fishing mortality. In production models, B_0 is also known as carrying capacity. It is often used as a biological reference point in fisheries management.

Stock Structure: the structure of a particular stock, in terms of its size or age composition.

Stock-Recruitment Relationship (SRR): the relationship between the level of parental biomass (e.g. spawning stock biomass) and subsequent recruitment level. Determination of this relationship is useful for fish population dynamics, since it represents nature's regulation of population size, whether or not the populations are being exploited.

Stock: fish stocks are subpopulations of a particular species of fish, for which intrinsic parameters (growth, recruitment, mortality and fishing mortality) are the only significant factors in determining population dynamics, while extrinsic factors (immigration and emigration) are considered to be insignificant.

Sustainable Fishing: fishing activities that do not cause or lead to undesirable changes in the biological and economic productivity, biological diversity, or ecosystem structure and functioning from one human generation to the next.

Yield: the yield curve is the relationship between the expected yield and the level of fishing mortality.

Declaration

I hereby declare that this submission is entirely my own work except where due acknowledgement is given.

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